

A MORPHOSPACE ODDITY: ASSESSING  
MORPHOLOGICAL DISPARITY OF THE CIMOLODONTA  
(MULTITUBERCULATA) ACROSS THE CRETACEOUS-  
PALEOGENE EXTINCTION BOUNDARY.

By

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Title of Study: A MORPHOSPACE ODDITY: ASSESSING MORPHOLOGICAL DISPARITY OF THE CIMOLODONTA (MULTITUBERCULATA) ACROSS THE CRETACEOUS-PALEOGENE EXTINCTION BOUNDARY.

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Abstract:

In this study, I focus on the loss of species diversity – and therefore morphological diversity - within the Cimolodonta (Multituberculata) during the Cretaceous-Paleogene (K-Pg) extinction, followed by their recovery in the Puercan (earliest Paleogene). Teeth make up the majority of the cimolodontan fossil record, allowing inferences of dietary ecology, body size estimates, and phylogenetic proximity. I analyzed morphological disparity within the restricted phylogenetic framework of the Cimolodonta. I addressed 3 questions: 1) Did the conditions of the K-Pg extinction select for or against cimolodontan dental morphologies, if it was selective at all? 2) Do levels of cimolodontan morphological similarity return to pre-extinction levels in the Puercan? 3) Do the Puercan Cimolodonta recover morphology lost during the extinction, or do the Cimolodonta morphologically diverge from the pre-extinction morphospace? I used Euclidian inter-taxon distance measures derived from dental character data to perform a principal coordinates analysis (PCO), generating a multidimensional representation of morphological similarity. To assess the selectivity versus non-selectivity of cimolodontan extinction across the K-Pg boundary, I analyzed the axes of the morphospace for morphological character gradients. I tested for extinction selectivity to determine the probability of generating the survivor-specie morphospace by chance. These results

indicate significant ( $P = 0.0006$ ) selection affecting cimolodontan survival across the K-Pg extinction. Overall morphospace occupation changed significantly ( $P < 0.015$ ) in the Puercan as well. I attribute this change in morphospace occupation to the diversification of the Taeniolabididae and incomplete recovery of Late Cretaceous morphospace by the Puercan Cimolodonta. Vacancies in the Puercan cimolodontan morphospace may be a result of changes in available dietary resources, or competitive exclusion. The Taeniolabididae occupy a morphospace region distant from the remainder of the Puercan Cimolodonta, supporting independent studies suggesting they were an immigrant taxon rather than a product of rapid phenotypic divergence. My results indicate selection taking place over the K-Pg extinction for small body size within the Cimolodonta. I also find evidence of partial reoccupation of Late Cretaceous cimolodontan morphospace in the Puercan, indicating ecological niche recovery.

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## CHAPTER I

### A MORPHOSPACE ODDITY: ASSESSING MORPHOLOGICAL DISPARITY OF THE CIMOLODONTA (MULTITUBERCULATA) ACROSS THE CRETACEOUS-PALEOGENE EXTINCTION BOUNDARY.

#### I. INTRODUCTION

In this study I focus on the North American *Cimolodonta* (Multituberculata), an extinct sub-order of herbivorous/omnivorous mammals which arose prior to the split of the Metatheria and Eutheria (Kielen-Jaworowska and Hurum 2001; Rose 2006). Thriving for over one-hundred million years, the Multituberculata exceed all other mammalian orders, both extinct and extant, in longevity (Van Valen and Sloan 1966; Weil and Krause 2007). Exceptional in both lineage diversity and prevalence in the fossil record, the Multituberculata are employed as biostratigraphic markers throughout their range (Weil and Krause 2007). In North America, the Puercan diversity recovery of the Multituberculata is composed entirely of the multituberculate sub-order *Cimolodonta*, which originated in the middle Cretaceous (Kielan-Jaworowska et al. 2004; Weil and Krause, 2007).

Appearing in the Aptian/Albian (126.3 -112 Ma/112-100.5 Ma) (Ogg 2012; Rose 2006) and diversifying in the latter half of the Cretaceous (Wilson et al. 2012), the Cimolodonta lost over half of their taxonomic diversity during the Cretaceous-Paleogene (K-Pg) extinction 65.95 Ma (Vandenbergh, et al. 2012; Weil and Krause 2007; Wilson et al. 2012). Cimolodontan fossil teeth used in this study are predominantly found in Western North America, East of the Rocky

Mountains (Figure 1). The Western Interior Seaway and Rocky Mountains limited the extent of their longitudinal range in the Cretaceous, with only those living in the fossil-forming depositional basins now represented in the fossil record (Figure 1).

Taxonomic loss during the K-Pg extinction does not set the Cimolodonta apart from other mammalian taxa of the end-Cretaceous; rather it is their ensuing recovery. Following the K-Pg extinction, the Cimolodonta eventually recovered the taxonomic diversity lost only a few million years prior (Weil and Krause 2007). The uniqueness of this response begs the investigation of how the Cimolodonta reacted to the conditions of their Puercan (65.9-63.3Ma) post-extinction environment. Was extinction selective in its effects, acting primarily on specific morphologies or morphotypes, or did taxonomic losses occur across all morphologies and occupied ecospace? Did the recovery of damaged ecosystems result in recovery of morphologies lost during the extinction? Are taxon morphologies more or less disparate in the Puercan, and what does this infer about cimolodontan recovery? To investigate this, I will evaluate disparity of the North American Cimolodonta (Multituberculata) across the K-Pg extinction boundary using dental morphology and taxonomy.

The evaluation of shifting morphological traits in relation to taxonomic diversity of a chosen group of taxa is termed disparity (Brusatte et al. 2008; Erwin 2006; Foote 1997; Grass 2009; Jernval et al. 1996; Lupia 1999; Wills 2001; Wills 1994). I have used principal coordinate analysis (PCO) of a discrete dental character matrix converted into a Euclidian distance matrix as the basis for morphospace construction. Here morphospace is the range of points, each representing a suite of dental characters for a single taxon, existing within the region defined by

the PCO axes. This differs from ecospace, also an important consideration for this study, in that ecospace changes are inferred from morphospace changes. Morphospace is modeled directly from the discrete morphological data. As changes in ecospace are inferred from shifts in morphospace occupation, it is important to note that morphospace changes are attributed to changes in a given taxon's ecosystem. To put shortly, changes in an ecosystem exert selective pressure on organisms, in this case on dental characters. As an ecosystem changes, available ecospace will shift. Changes in available ecospace may influence inter- and intraspecific competition, therefore altering – positively or negatively - the competitive advantage of present morphologies. The data set used in this study is made entirely of dental characters; therefore any evolutionary changes in morphospace are limited to characteristics that may be inferred from only teeth.

I infer changes in ecospace occupancy through ecosystem-mediated morphotype selection over the K-Pg extinction boundary by analyzing changes in morphospace occupancy, and morphological disparity metrics range, variance, nearest neighbor distances (NND) (Figure 2), non-parametric multivariate analysis of variance, rarefaction, and jackknife procedures. Set in the context of catastrophic damage to floral and faunal communities that occurred at the K-Pg boundary, I evaluate taxonomic and morphological radiation, and how the entirety of ecological recovery may drive the evolution of cimolodontan disparity in the Puercan North American Land Mammal Age (NALMA) of the Paleocene. I also assess cimolodontan morphospace change as a result of the end-Cretaceous mass extinction, in hopes of revealing biological factors that contributed to their loss of diversity. I use the NALMAs Judithian (79 - 74 Ma), Edmontonian (74 - 67.5 Ma), and Lancian (67.5 - 63.3 Ma) to make up the pre-extinction partition of cimolodontan dental data; the Puercan (65.9 - 63.3 Ma) is the only NALMA included for the

post-extinction partition (Cifelli et al. 2004; Lofgren et al. 2004; Ogg 2012; Vandenberghe et al. 2012). When an environmental cataclysm occurs, such as the Chicxulub asteroid strike at the K-Pg extinction boundary, large portions of available ecospace are eliminated by habitat destruction. This has a greater impact than gradual ecosystem shifts or extinction derived from interspecific competition, which imposes selection on populations. This is because in cataclysmic events the ecospace itself may be eliminated, as are any taxa inhabiting it (Wills 1994). As a damaged ecosystem recovers and stabilizes, previous regions of ecospace may recover, and new ecospace may be realized. This will mean that taxa re-diversifying as the ecosystem recovers will be unlikely to occupy the exact same region of eco or morphospace as members of that lineage did prior to the cataclysm (Wills, 2001; Wills et al., 1994). Alternatively, ecospace may be eliminated, or taken up by an unrelated taxonomic group resulting in competitive exclusion from ecospace. In these cases, a recovering taxon would not necessarily recover the morphospace it occupied prior to extinction, as the ecospace space that favored that morphotype is no longer available.

Changes in available ecospace in the wake of a mass extinction may be detectable by changes in the morphospace occupied by surviving taxa. In a case where one or more regions of ecospace are eliminated, changes to the range of morphospace represented within the PCO analysis are expected (Wills 2001). This is the result one would expect in a case of selective extinction, where taxa expressing a specific dental character or suite of dental characters become vulnerable (Wills 2001). Elimination of taxa on the periphery of morphospace, reducing morphospace range, would indicate selection against specialized forms over generalist taxa.

Similarly, directional expansion of morphospace over time would indicate selective specialization (Wills 2001).

An extinction on the scale of the K-Pg may have been non-selective, affecting taxa from all regions of ecospace and therefore across morphospace. In non-selective extinction (Figure 3), changes to variance and nearest neighbor distance are expected over changes in range (Wills 2001). Variance and nearest neighbor distance disparity metrics are closely related, as both indicate taxonomic losses throughout the inhabited morphospace. The difference is in how relative point position is assessed; variance is concerned with the total degree of spread within a given lineage morphospace. Nearest neighbor distance assesses the amount of smaller point-clusters, and how tightly packed they are, within that same morphospace (Wills 2001). Nearest neighbor distance is more sensitive to smaller scale groupings than to overall distribution in morphospace (Wills 2001). Damage to an entire ecosystem, as opposed to portions of it as expected to explain range changes, would result in changes to variance and nearest neighbor distances as taxonomic losses are scattered throughout morphospace. In these cases, changes to range are possible, but not likely to be as extreme. A lack of change in range, variance, or nearest neighbor distance between chronological bins serves as the null model for this study. An absence of visible change in morphospace occupation would imply a lack of change in ecospace availability. Morphospace turnover through chronological bins without significant change in range or variance of occupied morphospace is more likely based on non-selective extinction (Wills 2001).

In cases where cimolodontan recovery following the K-Pg extinction results in the reoccupation of vacated morphospace, paleocommunity data can be used to determine change or

continuity of resources that may favor specific morphotypes. Data on last appearance times and diversity of flora and insects may be indicative of changes in multituberculate diet. Differential recovery of these food resources will help interpret changes in morphospace occupation as derived from PCO analysis, as all characters being used are dental.

In this study I ask three questions: 1) Did the conditions of the K-Pg extinction select for or against certain cimolodontan morphologies, if it was selective at all? 2) Did taxonomic recovery return variance and range to pre-extinction conditions within morphospace? 3) Do Puercan cimolodontan species re-populate the morphospace of eliminated subgroups, disperse in close proximity to remaining occupied morphospace, or appear in a previously uninhabited region of morphospace? Answers to these questions will provide insight to the loss and subsequent recovery of cimolodontan taxa during the K-Pg extinction and Puercan. This research provides a unique opportunity to observe a large-scale regional extinction followed by initial recovery of taxonomic diversity within a single mammalian order, a circumstance rare if not singular in the mammalian fossil record.

### The K-Pg Extinction and Plant Communities

The K-Pg extinction event, stratigraphically marked by a layer of ash, clay, and other ejecta from the Chicxulub impact crater, bounds the end of the Cretaceous (144 Ma – 65.95Ma) and the beginning of the Paleocene (65.95 Ma – 55.8 Ma) (Alvarez et al. 1980, 1995; Hildebrand et al. 1991). Wilf and Johnson (2004) report a 57% loss of plant species over the K-Pg extinction boundary, with no notable recovery of diversity until the early Eocene. This damage to floral communities would have repercussions throughout every North American trophic chain. A massive ecological disruption would favor early successional floral regimes, as has been

confirmed by palynology studies (Johnson 1992). Johnson (1992) demonstrated a spike in gymnosperm spores in the earliest Paleocene, coincident with a drop in angiosperm diversity (Frederiksen 1994). This suggests a shift away from the open canopy forest of the late Cretaceous of North America, though Frederiksen (1994) also suggests this early successional regime of gymnosperms rapidly gave way to dense rainforest in the Paleocene. This drop in angiosperm would carry with it a hypothetical drop in food resources provided, including fruits, nuts, and seeds.

With drastic losses to primary producers such as gymnosperms and angiosperms, food variety and availability likely dwindled (Johnson 1992). Damage to floral communities would result in damage to terrestrial herbivorous arthropod (phytophagous insects) diversity and abundance, as most have a narrow range of flora they feed upon (Labandeira et al. 2002; Wilf 2008). The record of insect herbivore-damaged fossil leaves indicates a decrease in specialized phytophagory over the K-Pg boundary, possibly a result of losses in floral community taxonomic diversity (Labandiera et al. 2002). However, arthropod family-level diversity as judged by body-fossils remains stable over the K-Pg extinction event (Labandeira and Sepkoski 1993). This is potentially a picture of morphological and ecological disparity rather than generic or species-level diversity (Labandeira and Sepkoski 1993).

The biotic and ecological changes following the end-cretaceous extinction event were accompanied by an increase in placental mammalian diversity (Springer et al. 2003; but see O’Leary et al. 2013 for a dissenting argument). Most crown Placentalia orders originated in the Cretaceous, while intense interordinal diversification did not occur until the Paleogene (Springer et al. 2003). This Long Fuse Model of eutherian diversification (Springer et al. 2003) can be

explained by intense habitat disruption and niche evacuation during the K-Pg extinction; opportunities for speciation through ecological partitioning would have been plentiful immediately after the extinction (Alroy 1999; Alroy et al. 2000); however, see O’Leary et al. (2013) for evidence supporting the Springer et al. (2003) Explosive Model of Eutherian diversification. Taxonomic diversification of the Cimolodonta, following their diversity crash at the end of the Cretaceous, will be analyzed in this study through morphological disparity, allowing assessment of both taxonomic and morphological diversity before and after the K-Pg extinction.

#### Multituberculates as a Model Clade

The multituberculates avoided extinction at the close of the Cretaceous, though roughly fifty percent of their taxonomic diversity was lost in the K-Pg extinction event (Weil and Krause 2007). This was followed by a re-diversification in the Puercan, in which their diversity exceeded that recorded for the Cretaceous (Weil and Krause 2007; Wilson et al. 2012). The systematics of the Multituberculata remains unresolved, mostly due to preservational bias that has provided far more dental than cranial or postcranial material (Weil and Krause 2007; Kielan-Jaworowska et al. 2004). Because of this, all discussion and conclusions presented are limited to dentition and dentally inferred characteristics of cimolodontan biology and ecology.

In the collapse and subsequent re-diversification of the North American Cimolodonta following the K-Pg extinction, diversity of morphological features may have changed to suit new ecological requirements. Appearance of “new” cimolodontan species may be a result of population migration, when climate change led to range expansions and contractions (Weil 1999; Weil and Krause 2007). These species, previously inhabiting areas lacking fossil-forming



conditions, may have relocated to regions more taphonomically favorable for fossilization (Weil 1999; Weil and Krause 2007). Under this scenario, the initial rediversification of the Cimolodonta may be a taphonomic artifact. This does not discount a subsequent taxonomic radiation of immigrated taxa, nor does it imply that the extinction of the Multituberculata was a relocation of the clade back into taphonomically unfavorable habitats.

## II. METHODS

This study of the Cimolodonta uses a binary phylogenetic matrix of discrete dental characters, drawing from the NALMAs Judithian, Edmontonian, and Lancian under the heading of Late Cretaceous group of cimolodontan dental data (Appendix 1) (Cifelli et al. 2004; Lofgren et al. 2004; Ogg 2012; Vandenberghe et al. 2012); the early lower Paleogene Puercan NALMA makes up the post-extinction partition (Lofgren et al. 2004). The Judithian does not share a boundary with the K-Pg extinction, but is included to assess morphological changes occurring in the Cimolodonta prior to the Latest Cretaceous running up to the K-Pg extinction. The pre and post-extinction groups are used in assessing morphological disparity of the Cimolodonta on each side of the K-Pg extinction boundary. Metrics and data processing tools used for analyzing disparity follow techniques outlined by Brusatte et al. (2008), Erwin (2007), Lupia (1999), Wills (2001), and Wills et al. (1994).

Character data from 44 cimolodontan species (Appendix 2) have been drawn from multiple specimens and therefore multiple populations of each species (Weil 1999). Character scoring has been altered to binary from multistate to fit the requirements of the Principal Coordinates Analysis (PCO) and Non-Parametric Multivariate Analysis of Variance (NPMANOVA) used in this study (Anderson 2001). Dr. Anne Weil has provided the

phylogenetic dental character matrix analyzed in this study. Discrete multistate phylogenetic characters were partitioned in to a series of separate presence/absence or categorical binary characters. Continuous multistate characters were divided in to multiple categorical variables (Appendix 3). Species included in the initial data set that fell outside of the North American geographic and Judithian –Puercan (83.5-61.7 Ma) age parameters for the study were removed. All multistate scored characters have been converted to binary characters, as per the requirements of the R Euclidian distance calculating function VEGDIST (Oksanen 2010). *Cimexomys magnus*, *Cimolomys trochuus*, *Nidimys occultus*, *Paressonodon nelsoni*, *Catopsalis foliatus*, *Neoplagiaulax kremnus*, *Parectypodus vanvaleni*, *Parectypodus armstrongi*, *Neoplagiaulax macintyreii* are included in the data set with no more than 1/3 of included characters scored. Species with less than one-third of scored characters available have been retained, as inter-species distance values are calculated using only those characters that are present and scored (Oksanen 2010).

I compiled the discrete morphological character data into a usable data matrix with Microsoft Excel and the open source programming platform R (Claramunt 2010, Crawley 2009, Oksanen 2010, Paradis et al. 2003). Flexible, user-created script packages in R, specifically those for performing single and multivariate statistics and ordination procedures, make it an ideal platform for the range of analyses and data transformations performed in this study. The R packages VEGAN (Oksanen 2010) and APE (Paradis et al. 2003) were used to generate a Euclidian distance matrix, using the *VEGDIST* (Oksanen 2010) function on an imported .csv file edited in Excel.

Euclidian distance matrices describe character state-based differences between any two respective species in the form of a Euclidian distance measure, which is calculated at each character using binary scores (Gotelli and Ellison 2004; Wills 2001; Wills et al. 1994). Instances in which a character state is unknown resulted in that character being factored out for both species (Oksanen 2010). The distance matrix was subjected to a principal coordinates analysis (PCO), which uses linear distance metrics such as Euclidean instead of variable covariance (Wills 2001) which is used in Principal Components Analysis (PCA) (Gotelli and Ellison 2004; Zuur et al. 2007).

#### Principal Coordinate Analysis

I used Principal Coordinates Analysis (PCO), also known as Metric Multi-Dimensional Scaling and Classical Scaling, to calculate and visualize inter-species distances, and therefore show overlap, and separation, in morphospace occupation (Brusatte et al. 2008; Gotelli and Ellison 2004; Zuur et al. 2007). PCO is comparable to Principal Components Analysis (PCA) as it reduces data dimensionality of multivariate data through variable reduction, while maintaining spatial relationships between data points (Legendre and Legendre 1998); PCO does not create a bi-plot of variables and observations, and does not retain association of axes (eigenvectors) with specific independent variables, as PCA does (Zuur et al. 2007). However, PCO is superior when dealing with binary data types such as the morphological character presence/absence data used here (Legendre and Legendre 1994; Zuur et al. 2007), as its scaling methods are superior to correlation, covariance, and chi-squared methods, which are incorporated into PCA. Non-metric multidimensional scaling is superior to PCO in compressing distance relationships into 2-3 dimensions, but is also much more computationally intensive (Zuur et al. 2007).

PCO operates through the input of a distance matrix. I have used a Euclidean distance calculation (Gotelli and Ellison 2004; Legendre and Legendre 1998) applied to a binary morphological character matrix. Euclidean distance is determined by applying the Pythagorean theorem ( $d_{ij} = ((y_{i1} - y_{j1})^2 + (y_{i2} - y_{j2})^2 + \dots (y_{in} - y_{jn})^2)^{1/2}$ ) to the binary character data matrix;  $n$  is the number of morphological characters used to determine the distance between any two species,  $i$  and  $j$  are the individual species, and  $d_{ij}$  is the straight-line distance between the two species in an  $n$ -dimensional space (Gotelli and Ellison 2004). This calculation results in an  $n$ -species  $\times$   $n$ -species inter-species distance matrix  $D$ , which is transformed via a dimensionality-reducing, double-centering procedure into a coordinate matrix  $D^*$  via the formula  $d^*_{ij} = -(1/2)d^2_{ij}$  (Gotelli and Ellison 2004; Gower 1967). This coordinate matrix  $D^*$  is then transformed into matrix  $F$ , through the formula  $f_{ij} = d^*_{ij} - \bar{d}^*_i - \bar{d}^*_j + \bar{d}^*$  (Gotelli and Ellison 2004; Zuur et al. 2007). Here,  $\bar{d}^*_i$  and  $\bar{d}^*_j$  are the means of row  $i$  and column  $j$ , respectively, and  $\bar{d}^*$  is the mean of the matrix  $D^*$  (Gotelli and Ellison 2004; Zuur et al. 2007). This double-centering procedure, transforming the inter-species distance matrix  $D$  to coordinate matrix  $D^*$ , and then to matrix  $F$ , is followed by the eigenvalue decomposition procedure, also called spectral decomposition (Legendre and Gallagher 2001). From this, eigenvectors are calculated, providing vectors of principal coordinates which are the position of each species included in the analysis on respective eigenvectors (Gotelli and Ellison 2004). A specific eigenvalue is calculated for each eigenvector (Brusatte et al. 2008; Wills et al. 1994). The eigenvalues expresses the amount of variance in the original distance matrix explained by the respective eigenvector (Brusatte et al. 2008; Wills et al. 1994). I used PCO eigenvector and eigenvalue outputs to visualize morphospace occupation, change in positioning of the centroid, and perform range, variance, nearest neighbor distance, non-parametric multivariate analysis of variance (NPMANOVA), and jackknife resampling calculations (Brusatte

et al. 2008, Wills 2001, Wills et al. 1994). I cut off the described variance (relative eigenvalues) of the summed eigenvectors at 0.90, following the methods of Brusatte et al. (2008) and Wills et al. (1994). All eigenvectors beyond those first 17 that explain 90.94% of the variance are not considered in any calculations or visualizations.

#### Geometric Means of Disparity Metrics (Range, Variance)

The morphospace range metric for disparity assesses the extent of morphological derivation, as well as breadth of morphotypes present (Wills 2001). A taxon plotting on the edge of morphospace is considered more derived along a single axis, or along multiple axes, than a taxon closer to the median (Wills 2001). Each axis contains an unknown number of morphological characters from the original morphological character data. However, post-hoc assessment of relative taxon positioning can reveal morphological components of axes defining the morphospace. Range is frequently conveyed as a sum or product value, as it is a measure of breadth across multiple dimensions (Brusatte et al. 2008). Sum of range is calculated by adding the lengths of eigenvectors, while product of range is calculated by multiplying axis lengths (Wills 2001). Sum and product measures both reflect changes in morphospace occupation without value transformation before or after calculation. While not interchangeable, they are similar enough to warrant doing one or the other, while not necessitating both (Brusatte et al. 2008). These same considerations hold true for the variance disparity metric. Here I have chosen to use the sum measure.

The geometric mean of range provides average values for the occupied 17-dimensional morphospaces; the geometric mean of variance gives an average measure of species dispersion within the respective 17-dimensional morphospaces (Brusatte et al. 2008; Wills 1998). Geometric

means for range are calculated by taking the 17<sup>th</sup> root of the sum of range values, using custom-created R-script; the 17<sup>th</sup> root is taken to account for the 17 dimensions range is calculated across.

Variance is determined by calculating the standard deviation of species dispersion within the 17 dimensional morphospace, using the R command VAR (Crawley 2009). It should be noted, the range and variance disparity metrics are not intended as indicators of functional convergence, or levels of evolution, but as measures of morphospace occupation and dispersion (Wills 1998). However, taxon proximity and dispersion within morphospace have ecological consequences that may be inferred.

#### Rarefactions of Range and Variance Metrics

The purpose of rarefaction is to apply a single metric to groups of different sizes, controlling the effect of group size on range and variance disparity metrics. As group size increases, there is increasing chance that range and variance will go up simply due to increased numbers of different species (Brusatte et al. 2008; Foote 1992; Wills et al. 1994; Wills 2001; Krebs 1999). The range metric assesses the minimum and maximum principal coordinate values on each of the 17 included eigenvectors among all included species, establishing the boundaries of the 17-dimensional morphospace (Wills 2001). These range values are summed (sum-range) to give a single term that represents the magnitude of range within the assessed 17-dimensional space. In biological language, range shows the peripheral extents of morphological variation, as a group with a large range value contains more highly disparate and therefore peripheral taxa than a group with a low range value (Wills 2001). The range metric is complicated by variation in inter-taxon scatter within morphospace; a group with a high range value may have a small number of outlying taxa bounding the morphospace (Wills 2001). Such beguiling distribution problems can

mostly be dealt with through the rarefaction procedure, but a more complete understanding of morphospace structure, and taxon distribution within, can be assessed with the variance metric (Brusatte et al. 2008; Wills 2001).

Rarefaction of variance (standard deviation from the arithmetic mean) reveals change in inter-species scatter with increasing sample size; this spacing measure indicates degrees of morphological separation within the 17-dimensional morphospace (Brusatte et al. 2008; Claramunt 2010; Wills 2001). Species sampling for range and variance metrics from each chronological group has been set to 15, reduced from 24 for pre-extinction taxa and 24 for post-extinction species. This reduced sample size is in response to concerns of over-fitting the rarefaction relative to the data being sampled. Separate rarefactions for range and variance metrics have been run for each chronological group, each applied to the first 17 most explanatory eigenvectors, accounting for 90.94% of the total variance in the PCO.

The variance metric is a measure of global inter- species distance, or taxon scatter (Wills 2001). Species scatter is a result of morphological dissimilarity among taxa within morphospace. Low variance within morphospace indicates high morphological similarity between all taxa (Wills 2001). High variance can result from wide scatter in morphospace, indicating greater morphological dissimilarity among taxa in the morphospace being assessed (Wills 2001). Increased variance can also result from taxa plotting mostly along the edges of the morphospace (Wills 2001).

## Nearest Neighbor Distance

Clustering can create problems for both range and variance metrics; nearest neighbor distance calculations can be used to address this (Wills 2001). First order NND is used to express cladistic similarity, based on PCO-transformed morphological characters (Wills 1998; Wills 2001). Using principal coordinates of the first three most explanatory eigenvectors (43.04% of the total variance), nearest neighbor distances within the PCO morphospace were calculated for the Late Cretaceous and Puercan Cimolodonta faunal partitions. The advantage of NND values, relative to range and variance disparity metrics, is the focus on localized relationships between taxa (Wills 2001). NND values are plotted, using a minimally spanning tree to connect nearest neighbors within three-dimensional space, in a scatterplot using the first three most explanatory eigenvectors as axes (Wills 1998; Wills 2001; Wills et al. 1994). This method maximizes variance accounted for, while keeping the figure easy to read (which can become difficult with truly three dimensional NND plots). R script for this analysis is adapted from an NND procedure outlined in Crawley (2009). Geometric mean of NNDs is calculated by taking the twenty-fourth root of pre and post-extinction cimolodontan NND; the 24<sup>th</sup> root is taken because there are 24 cimolodontan species on each side of the extinction boundary. Change in the NND distribution was tested for significance using the Mann-Whitney rank-sum test (Crawley 2007).

## Non-Parametric Multivariate Analysis of Variance

The non-parametric multivariate analysis of variance (NPMANOVA) is used to determine significance of separation between multivariate means (centroids) of multiple dependent variables grouped by one or more independent variables (Weinfurt 2009). When performing multivariate analysis of variance on non-parametric data sets, as used here, random



resampling methods are needed to induce normality, while not violating the parametric provisions of the MANOVA (Anderson 2001; Gotelli and Ellison 2004; Weinfurt 2009). This is the difference between the standard MANOVA and the NPMANOVA. The advantage of a MANOVA procedure over multiple ANOVA's is two-fold: first, the single MANOVA reduces the chance for type 1 error, relative to the multiple ANOVA's (Weinfurt 2009); second, the ability to incorporate multiple dependent variables in a MANOVA method, which is essential to the use of multiple eigenvectors (Weinfurt 2009). The NPMANOVA has been performed in R using the *ADONIS* command, found within the VEGAN package (Oksanen 2010).

Dependent variables are the PCO scores along respective eigenvectors. Differences in centroid position between the independent variables, the pre and post-extinction groups, are interpreted as differences in group position within the morphospace (Brusatte et al. 2008, Gotelli and Ellison 2004). Chronological groups of species are broken down into Late Cretaceous (83.5-65.95 Ma), and Puercan (65.95- 63.3 Ma). Thus, pre-extinction (83.5-65.95 Ma) and post-extinction (65.95-61.7 Ma) chronological groups are used to group species exclusively found on each side of the K-Pg extinction boundary (Cifelli et al. 2004; Lillegraven and McKenna 1986; Lofgren et al. 2004). Those present before and after the extinction are grouped separately as boundary-crossing species.

#### Jackknife

Jackknife analysis is used to infer random versus non-random extinction and diversification by way of random species sampling. Four species (*Cimexomys minor*, *Mesodma formosa*, *Mesodma garfieldensis*, *Mesodma thompsoni*) of those included in analyses survived the K-Pg extinction; to estimate randomness of species survival, and therefore selective versus non-

selective extinction, a jackknife procedure using 5,000 sampling iterations was applied. Pre-extinction species (including survivors and those lost in the extinction) were sampled without replacement. Selective extinction would result in a significant decrease in morphospace range, as well as inter-species variance. This procedure compares the range values of survivor species with the range and variance of 5,000 random samples of the pre-extinction species to determine if extinction was random or non-random. Post-extinction species (without species that survived across the K-Pg extinction boundary) were sampled without replacement to assess rediversification in the Puercan. Conservative re-diversification where pre-extinction levels of competitive and selective pressure were the same or elevated would likely result in the range of the four randomly selected species being close in value to the survivor species. I used the observed sum-range distribution of pre-extinction species and the calculated survivor species range of morphospace mean (Gotelli and Ellison 2004) to test for the significance of reduced sum-range morphospace occupation during the K-Pg extinction.

### III. RESULTS

PCO analysis yielded 17 eigenvectors to explain 90.94% of the total variance (table 1). All analyses were therefore limited to these first 17 most explanatory axes. The remaining 9.06% of the variation is explained by 26 remaining eigenvectors (Table 1). No substantial benefit would result in using additional eigenvectors that each contributes no more than 1.18% variance explained, and therefore these additional vectors are excluded from the disparity analysis.

The shifted morphospace occupation of the Cimolodonta across the Cretaceous-Paleogene (K-Pg) extinction boundary is summarized in Figure 4, and shown to be significant through the use of the NPMANOVA statistic (Table 2, Table 3). species surviving the K-Pg

extinction stretch along the first eigenvector axis of the morphospace, with minimal spread along the second axis (Figure 4A). Post-extinction morphospace range (Figure 4B) increases relative to the pre-extinction range. This increase in range is predominantly owed to the presence of the Taeniolabididae in the Puercan, which occupy a region of morphospace along the second axis that is unoccupied in the Late Cretaceous (Figures 4E, F). The Taeniolabididae are the only Puercan taxa to occupy a region of morphospace that was not occupied by Late Cretaceous taxa (Figures 4E, F). There is little change in morphospace occupation between the Judithian and Latest Cretaceous Edmontonian and Lancian (Figure 4C); this observation is corroborated by the NPMANOVA (Table 3).

Jackknife sampling the sum-range indicates an increase in morphospace range in the Puercan (Figure 5) as well as a non-random decrease of morphological disparity during the extinction. This non-random decrease of morphospace range is indicative of selective extinction acting on the Cimolodonta during the K-Pg extinction. In the Puercan, the frequency distribution has shifted to higher values relative to the pre-extinction morphospace range distribution. Frequency of the highest possible sum-range values decreases after the extinction, likely owing to the central morphospace gap. This central space was predominantly occupied by the Cimolomyidae prior to the K-Pg extinction, but failed to recover its previous level of taxon density in the Puercan.

Increased morphospace range after the extinction is corroborated and shown to be independent of sample size in the rarefaction of sum-ranges (Figure 6). Across values of  $n$ -species greater than or equal to two, the sum-range of occupied morphospace is higher after the K-Pg extinction than before the K-Pg extinction (Figure 6). Levels of variance before and after

the extinction are also found to be independent of sample size, via the variance rarefaction (Figure 7). In the rarefaction of variance, the Cimolodonta show greater inter- species scatter within the 17 dimensional morphospace after the extinction compared to before the extinction. Nearest neighbor distance of the Cimolodonta (Figure 8, Figure 9) also increased post-extinction, though not significantly ( $P = 0.9342$ ). Taking the geometric mean of NND across the 17 most explanatory eigenvectors, the post-extinction Cimolodonta demonstrate a non-significant increase in inter- species distances across ninety percent of explained variance (Figure 9). The third eigenvector of Figure 8 shows a shift from negative to positive values (white to black) in morphospace occupation across the K-Pg boundary. Average nearest neighbor distance increases post-extinction as well; standard deviation of NND is observably greater (Figure 8). The NND disparity metric therefore is in agreement with range and variance metrics, showing an increase in cimolodontan disparity following the K-Pg extinction. The increase in variance indicates greater distance between individual species overall, as well as greater dispersion between clusters.

The increase in cimolodontan disparity following the K-Pg extinction was coincident with a significant change in morphospace occupation across the 17 most explanatory eigenvectors (Table 2). Changes in range, variance, and dimensional weighting within morphospace shift the post- extinction centroid position away from the pre-extinction centroid location (Figures 4A, B). This shift in centroid position is found to be significant (Table 2), with the chronological group dependent variable below the 0.05 alpha. The genus assignment independent variable is significant across the data set ( $P = 0.0001$ ). A second NPMANOVA was run using discrete chronological groups as dependent variables (Judithian, Latest Cretaceous including Edmontonian and Lancian, and Puercan); a significant explanatory effect was found for the

Puercan, but not for the Judithian or Latest Cretaceous dependent variables. The interactive variable between the Judithian and Latest Cretaceous is also non-significant (Table 3). This significant shift of centroid position in the Puercan reinforces the increase in cimolodontan disparity following taxonomic losses during the K-Pg extinction.

#### IV. DISCUSSION

The cataclysmic ecological collapse at the close of the Cretaceous coincident with the K-Pg extinction greatly reduced the taxonomic diversity and morphological variation of the Cimolodonta. Taxa that survived - *Cimexomys minor*, *Mesodma garfieldensis*, *Mesodma thompsoni*, and *Mesodma formosa* - were isolated to a small region of the cimolodontan morphospace. The peripheral location of these survivor species within the pre-extinction morphospace implies that the K-Pg extinction affected nearly all morphotypes except for a small number of morphologically similar species (Wills 2001). These surviving multituberculates were small, with an M<sup>1</sup> length between 2 mm and 4 mm. This preservation of a small morphological pocket suggests that the taxonomic losses experienced by the Cimolodonta at the end of the Cretaceous were the result of selective pressure, in contrast to a random extinction. This non-random selective pressure may have been acting on a component of body size, possibly size-dependent dietary resources and their availability. Smaller cimolodontans would have lower absolute food intake requirements (Churchfield 2002; Nagy 1987), allowing them to survive on less of their various dietary resources than larger cimolodontans. However, it is not within the scope of this study to conjecture selective mechanisms not related to diet or food resources.

When considering dietary niches, it is important to remember that the realized dietary niche, along with the species-specific dentition, does not equal a fundamental niche of equal

breadth (Futuyma and Moreno 1988); the realized niche is narrower than the fundamental niche, due to local selective factors such as predation, competition, and resource types. The fundamental niche can be considered the totality of potential ecospace an organism could occupy, unimpeded by these factors (Futuyma and Moreno 1988). Shipley et al. (2009) discussed the existence of facultative and obligate dietary niches, which I believe is useful when considering likely generalist feeders such as multituberculates. Two categories from Shipley et al. (2009) stand out: facultative specialist, and facultative generalist. A facultative specialist would focus on a very narrow range of food types, but be physically capable of shifting to other food resources if the need arose. A facultative generalist is more flexible, consuming a broad variety of foods regularly, and able to easily adapt to changes in food availability (Shipley et al. 2009). These differences in dietary resource use can allow multiple generalist species to coexist by incorporating different amounts of available food resources into their diets, minimizing the effects of food resource competition (Meserve et al. 1988). Body size differences can also result in realized niche separation; a large and a small insectivore may both eat arthropods and annelids, but their differences in size mitigate competition due to differences in effort and energetic value for different sized prey (Churchfield et al. 1999). The same kinds of dietary niche separation can be achieved through differential habitat use, as demonstrated in tropical bats by Polly et al. (2007); temporal differences in foraging by dietary analogs can reduce interference competition as well as resource competition (Ray and Sunquist 2001; Vieira and Paise 2011).

Sudden decimation of habitat along with food resources may have destabilized any existing body size or temporal resource partitioning during the K-Pg extinction, pushing otherwise non-competing species into sudden strong resource competition (Campbell et al. 2007;

Ray and Sunquist 1983). Loss of specific food resources would first hurt obligate feeders, as they would have very narrow fundamental dietary niches (Shipley et al. 2009). Facultative generalists may have been driven to extinction by intensified resource competition combined with diminished resource availability. Decreased fecundity due to resource stress would also have negative effects.

Work by Nagy (1987) implies cimolodontans may have focused on insects and seeds as dietary resources, as both are shown to be of greater energetic value than foliage for eutherian and metatherian mammals. Modern passerine birds also receive a high energetic reward from insect consumption (Nagy 1987); presuming physiological continuity with relatives near the K-Pg boundary, small birds may have competed with cimolodontans for food resources. Insect, foliage, and seed food resources are known to recover quickly in modern damaged ecosystems (Krause 1982; Ray and Sunquist 2001). Having dietary flexibility increases the recovery potential in modern taxa inhabiting disturbed or fragmented habitats (Swihart et al. 2003). Therefore, the apparent rapid recovery of taxonomic and morphological diversity of the Cimolodonta may have been aided by a generalist-feeder dental morphology targeting a range of rapidly recovering dietary resource types.

#### Recovery in the Puercan

The findings of Wilson et al. (2012) indicate increasing disparity of the Multituberculata in the late Cretaceous, presumably to take advantage of novel or newly opened ecospace. Following the diversity drop during the K-Pg extinction, disparity quickly rebounded and peaked in the Multituberculata during the Paleogene. These patterns are in agreement with findings for the Cimolodonta in this study. Concentrations of cimolodontan species along the periphery of

morphospace are consistent before and after the K-Pg extinction event, though disparity of dental morphotypes is demonstrated to increase. This continuity of morphospace concentration before and after the extinction indicates that many resources utilized by the pre-extinction Cimolodonta recovered quickly in the Puercan. It is also possible that specific dietary resource loss was not responsible for the end-Cretaceous multituberculate extinctions; however, this analysis is limited to the consideration of characteristics related to teeth, as all data used is dental. First molar lengths of survivor species - *C. minor*, *M. garfieldensis*, *M. thompsoni* and *M. formosa* - indicate selection for cimolodontans with small body size during the K-Pg extinction.

The largest multituberculates, the Taeniolabididae, plot along the edge of the Puercan morphospace, and have the most negative values of any co-occurring taxon along the second eigenvector in a morphospace region unoccupied in by the pre-extinction taxa (Weil and Krause 2007). *C. minor*, *M. thompsoni*, *M. garfieldensis*, and *M. formosa* all plot with positive PCO values on the second eigenvector. *M. thompsoni*, *M. garfieldensis* and *M. formosa*, all members of the Neoplagiaulacidae, form the positive apex of the morphospace along the second eigenvector. The Neoplagiaulacidae are generally small, no bigger than a vole, with the genus *Mesodma* containing the smallest of the family (Weil and Krause 2007). The genus *Neoplagiaulax* contains the largest species of the Neoplagiaulacidae, with small values along the second axis indicating greater body size (Weil Krause 2007). This size-gradient along the second axis appears to have also have been a diversity gradient, as taxonomic richness increases moving from small and large to intermediate body sizes.

Post-extinction Cimolodonta recover within a similar region of morphospace as occupied before the K-Pg extinction, with the exception of morphospace occupied by the Taeniolabididae



and Cimolomyidae. This indicates that the predominant dietary makeup among the majority of the Cimolodonta, especially the Neoplagiaulacidae, changed little across the extinction boundary. This is likely an effect of a non-specialized dentition able to incorporate diverse food resources as biotic communities recovered. This reoccupation of morphospace by the majority of recovery taxa in the Puercan suggests rapid recovery of these dietary resources. Rapid recovery of dietary resources would allow survivor taxa to diversify morphologically into similar ecospace and therefore similar morphospace regions as before the extinction. For this to be true, dietary resource availability and content would need to be comparable before and after the extinction.

The Taeniolabididae occupy a region of Puercan morphospace that is uninhabited by the Cretaceous Cimolodonta. Weil and Krause (2007) suggest that the Taeniolabididae were obligate folivores, based on molar crown morphology as well as body size. This would explain the morphospace expansion facilitated by these taxa. The PCO places the Taeniolabididae far outside the morphospace occupied by the Late Cretaceous Cimolodonta. This indicates that the Taeniolabididae are either cases of rapid and intense phenotypic divergence across the K-Pg boundary, or are immigrant taxa from outside of the foreland basins East of the Rocky Mountains where cimolodontan fossils are found today. *Catopsalis* appears in the Puercan North American fossil record almost immediately after the K-Pg extinction, already derived from the known survivor taxa in dental morphology and large body size (Weil and Krause 2007). This immediate appearance in the fossil record, combined with innately disparate dental morphology, implies that *Catopsalis* and the Taeniolabididae were not derived from a K-Pg survivor taxon within the study area. Such phenotypic divergence would likely take longer to manifest in the fossil record, as would immigration from another continent such as Asia. More likely *Catopsalis* emigrated from

non-fossil forming habitats in the Rocky Mountains in to lowlands where deposition facilitated fossilization.

Studies of small mammal recovery following habitat disruption indicate that recovering populations are seeded from within the damaged region, not from undamaged outside patches (Vieira 1999). Trappings in the Brazilian Cerrado following fires have demonstrated small mammals using even the central-most portions of the damaged habitat (Vieira 1999). A similar study in Australia, also assessing small mammal recovery in areas damaged by wildfires, found extensive drops in population sizes following catastrophic fires, in some cases up to 88% losses in number of individuals (Banks et al. 2011). Their findings indicate population recovery through survivor breeding within the burned habitat, not recolonization from external unaffected habitat (Banks et al. 2011). On a much larger scale, these studies support the taxonomic recover of the Cimolodonta from within North America, as opposed to being facilitated by immigration.

It is noted that small mammal recovery following habitat disruptions are scale-dependent; habitat disruption of intense severity and extreme breadth of geographic area do not necessarily follow the same rules of geographically limited disturbances (Banks et al. 2011). Banks et al. (2011) suggests a “nucleated recovery”, where pockets of survivors are initially isolated, then as floral recovery ensues these clusters begin to comingle. In regions where populations are extirpated, or become reproductively extinct as opposed to damaged, recolonization is effectively the only option. Time scale and mechanism of the habitat disruption in modern communities is clearly not a complete parallel with the K-Pg extinction event. However, ecological principals of habitat recovery following disruption should be consistent regardless.

The Castle Rock flora from the Denver Basin provides evidence for pockets of habitat that may have gone mostly unaffected by the K-Pg extinction event or recovered extremely quickly after. The floral assemblage of Castle Rock is rich, resembling a mature tropical rainforest habitat (Wilf et al. 2006). This conflicts with the results of Johnson's (1992) study of the Fort Union and Upper Hell Creek formations in North Dakota, which showed extensive evidence for floral extinction at the K-Pg boundary.

Central morphospace occupied in the Judithian and Lancian, but lost in the Puercan, indicates the loss of an entire dietary resource over the extinction boundary, or competitive exclusion of the Cimolodonta from that region of ecospace. There is a reduction of taxa occupying negative value morphospace along the third eigenvector in the Puercan. This implies that, while not derived along the first two eigenvectors, the central taxa, mostly cimolomyidans, were derived along a character or suite of characters that were heavily selected against at the extinction boundary, and remained selected against in the Puercan. Competitive exclusion could interfere with dental character selection that would otherwise allow the Cimolodonta to reoccupy this niche space lost during the extinction.

Low levels of variance imply similar food resource exploitation across the Cimolodonta, both before and after the K-Pg extinction. High levels of variance, with decreased NND, would indicate disparate dietary specializations among taxonomic groups. The moderate increase in nearest neighbor distance after the extinction relative to the pre-extinction fauna indicates that dental character-state differences between taxa broadened, on average, between members of the Cimolodonta. Specifically the average distance between a given taxon and its closest relative

increased at both local and global levels within morphospace. This implies increased levels of dental derivation in post-extinction Cimolodonta fauna.

## V. CONCLUSIONS

In my assessment of cimolodontan disparity over the K-Pg extinction boundary, I have found evidence to support the following answers to questions posed in the introduction: 1) The extinction of the Cimolodonta at the end of the Cretaceous appears to have been selective, working against body size in particular. 2) Taxonomic recovery in the Puercan results in slight increases in variance and NND, with a greater increase in occupied morphospace range, relative to pre-extinction morphospace occupation. 3) Puercan Cimolodonta primarily reoccupies peripheral regions of pre-extinction morphospace, leaving a large chunk of central morphospace open. Only the Taeniolabididae appear to occupy a novel region of cimolodontan morphospace, and therefore ecospace. All other Puercan taxa inhabit morphospace regions occupied before to the K-Pg extinction.

The extinction at the end of the Cretaceous devastated terrestrial and marine ecosystems and biodiversity. The Cimolodonta suffered taxonomic losses, but survived in to the Paleogene to diversify and spread in the recovering ecosystems of North America. This study indicates the K-Pg extinction selected strongly against greater body sizes in the Cimolodonta, eliminating all but the smallest species.

<b>Eigenvector</b>	Eigenvalues	Relative Eigenvalues	Cumulative Eigenvalues	<b>Eigenvector</b>	Eigenvalues	Relative Eigenvalues	Cumulative Eigenvalues
<b>1</b>	66.9635	0.2106	0.2106	<b>22</b>	2.1174	0.0067	0.9544
<b>2</b>	39.6985	0.1249	0.3355	<b>23</b>	2.1117	0.0066	0.9611
<b>3</b>	30.1897	0.0950	0.4305	<b>24</b>	2.0545	0.0065	0.9675
<b>4</b>	20.7673	0.0653	0.4958	<b>25</b>	1.5053	0.0047	0.9723
<b>5</b>	20.3813	0.0641	0.5599	<b>26</b>	1.2908	0.0041	0.9043
<b>6</b>	16.2799	0.0512	0.6111	<b>27</b>	1.1619	0.0037	0.9800
<b>7</b>	13.7195	0.0432	0.6543	<b>28</b>	1.0773	0.0034	0.9834
<b>8</b>	13.4173	0.0422	0.6965	<b>29</b>	0.9736	0.0031	0.9864
<b>9</b>	12.1203	0.0381	0.7346	<b>30</b>	0.7923	0.0025	0.9889
<b>10</b>	11.5362	0.0363	0.7709	<b>31</b>	0.7728	0.0024	0.9914
<b>11</b>	9.1271	0.0287	0.7996	<b>32</b>	0.5967	0.0019	0.9932
<b>12</b>	7.5082	0.0236	0.8232	<b>33</b>	0.4709	0.0015	0.9947
<b>13</b>	7.0978	0.0223	0.8455	<b>34</b>	0.4371	0.0014	0.9961
<b>14</b>	6.1238	0.0193	0.8648	<b>35</b>	0.3585	0.0011	0.9972
<b>15</b>	5.8481	0.0184	0.8832	<b>36</b>	0.2587	0.0008	0.9980
<b>16</b>	4.4728	0.0141	0.8973	<b>37</b>	0.2203	0.0007	0.9987
<b>17</b>	3.8653	0.0122	0.9094	<b>38</b>	0.1340	0.0004	0.9992
<b>18</b>	3.7588	0.0118	0.9213	<b>39</b>	0.1280	0.0004	0.9996
<b>19</b>	3.2352	0.0102	0.9314	<b>40</b>	0.0764	0.0002	0.9998
<b>20</b>	2.6892	0.0085	0.9399	<b>41</b>	0.0491	0.0002	1.0000
<b>21</b>	2.5083	0.0079	0.9478	<b>42</b>	0.0118	0.00004	0.9999
				<b>43</b>	0.0021	0.00001	1.0000

Table 1. Principal coordinates analysis output of all 43 eigenvectors. Each eigenvector contains a series of values, the principal coordinates, one for each taxon, which orient the taxa along each axis. Assembly of two or more eigenvectors results in a multidimensional morphospace, with taxa positioned using respective principal coordinates. Relative eigenvalues give respective percent of total variance for each eigenvector; the total variance explained with each additional eigenvector is provided in the cumulative relative eigenvalues column. Eigenvalues for eigenvectors 1-17 sum to 90.94% of the total variance. Vectors 18-43 therefore account for less than 10% of the total variance, and have been excluded from all analyses in this study. No negative eigenvalues were calculated; therefore no corrections have been applied.

	Df	Sums of Sqs.	Mean Sqs.	F. Model	R <sup>2</sup>	P-Value
<b>Chron bin</b>	<b>1</b>	<b>9.37</b>	<b>9.36</b>	<b>2.22</b>	<b>0.03</b>	<b>0.015</b>
<b>Genus</b>	<b>18</b>	<b>178.50</b>	<b>9.92</b>	<b>2.35</b>	<b>0.62</b>	<b>0.0001</b>
<b>Residuals</b>	<b>24</b>	<b>101.25</b>	<b>4.22</b>		<b>0.35</b>	
<b>Total</b>	<b>43</b>	<b>289.13</b>			<b>1</b>	

Table 2. Statistical assessment of disparity: genus versus chronological bins; each species was coded as existing before (Late Cretaceous) after (Puercan), or crossing the Cretaceous-Paleogene extinction boundary. NPMANOVA results assess genus and pre/post extinction status as dependent variables explaining the distribution of species in the 17 dimensional morphospace. The NPMANOVA was subjected to 10,000 permutations. Genera tested are: *Catopsalis*, *Cimexomys*, *Cimolodon*, *Cimolomys*, *Essonodon*, *Eucosmodon*, *Kimbetohia*, *Meniscoessus*, *Mesodma*, *Microcosmodon*, *Neoplagiaulax*, *Nidimys*, *Paracimexomys*, *Parectypodus*, *Paressonodon*, *Parikimys*, *Stygimys*, *Taeniolabis*, and *Xyromys*. As a dependent variable, genus was included to act as a null model for the PCO procedure. If the genus dependent variable failed to reach a significant p-value, the validity of the PCO procedure would be called in to question. The distance matrix and principal coordinate calculations are meant to preserve morphological distance relationships present in the original phylogenetic data. The genus p-value is likely inflated due to numerous genera with very few included species. The p-value for the chron\_bin dependent variable confirms observations in Figure 4; the centroid position does change significantly across the K-Pg extinction boundary. This indicates a significant shift in morphological disparity in the Cimolodonta in the Puercan, following the extinction.

	Df	Sums of Sqs.	Mean Sqs.	F. Model	R <sup>2</sup>	P-Value
Puercan	1	15.25	15.25	2.39	0.06	0.010
Edmontonian+ Lancian	1	7.05	7.05	1.12	0.02	0.333
Judithian	1	8.71	8.76	1.38	0.03	0.165
Edmontonian+Lancian: Judithian	1	9.76	9.76	1.53	0.03	0.112
Residuals	39	248.30	6.37		0.86	
Total	43	289.12			1	

Table 3. NPMANOVA results assessing significance of variation in species distribution within the 17-dimensional morphospace. The Puercan age is the only dependent variable that yields a p-value less than the 0.05 alpha, indicating a significant change in morphospace occupation across the K-Pg extinction boundary. This significant shift may reflect the outlier status of the Taeniolabididae in the Puercan. However, the low number of Taeniolabididae outliers – only four – along with the permutational subsampling procedure that characterizes the non-parametric MANOVA, means the result is likely robust to these concerns. The Judithian, Edmontonian and Lancian are combined into a single interactive dependent variable to test for significant explanatory power of all pre-extinction species on the global morphospace. While it has a lower p-value than either the Judithian or Edmontonian+Lancian variables alone, it still fails to reach the 0.05 alpha value.

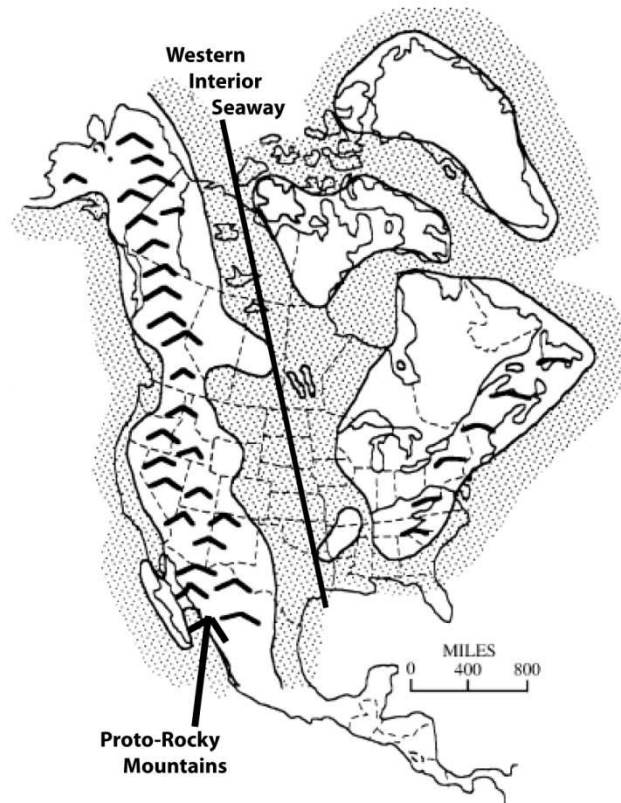


Figure 1. Late Cretaceous North America. Grayed regions represent marine environments.

Adapted from He et al. 2005.



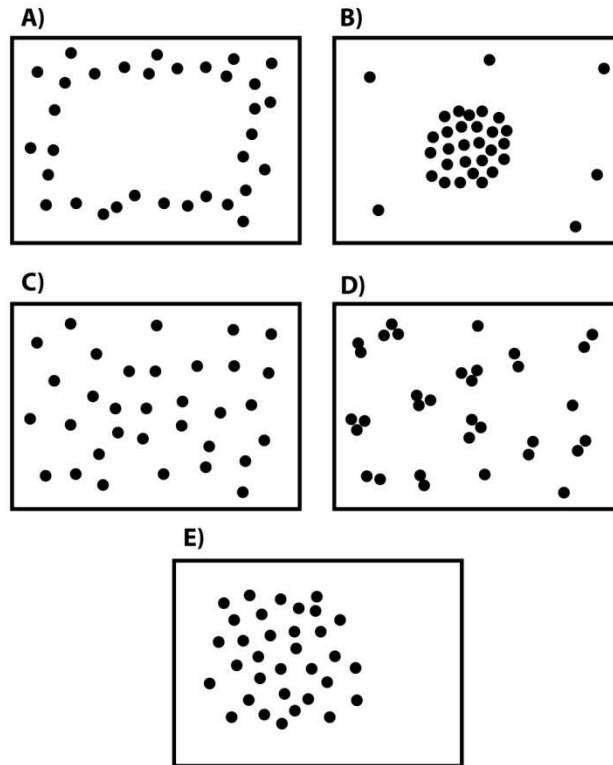


Figure 2. Range, variance, and nearest neighbor distance disparity metrics. Morphospaces A and B have equivalent ranges; variance of point position in morphospace B is lower than in A. Morphospaces C and D have equivalent variance; D exhibits decreased NND relative to morphospace C; the range of C and D is equal. Morphospace E has a decreased morphospace range relative to all other example morphospaces shown.

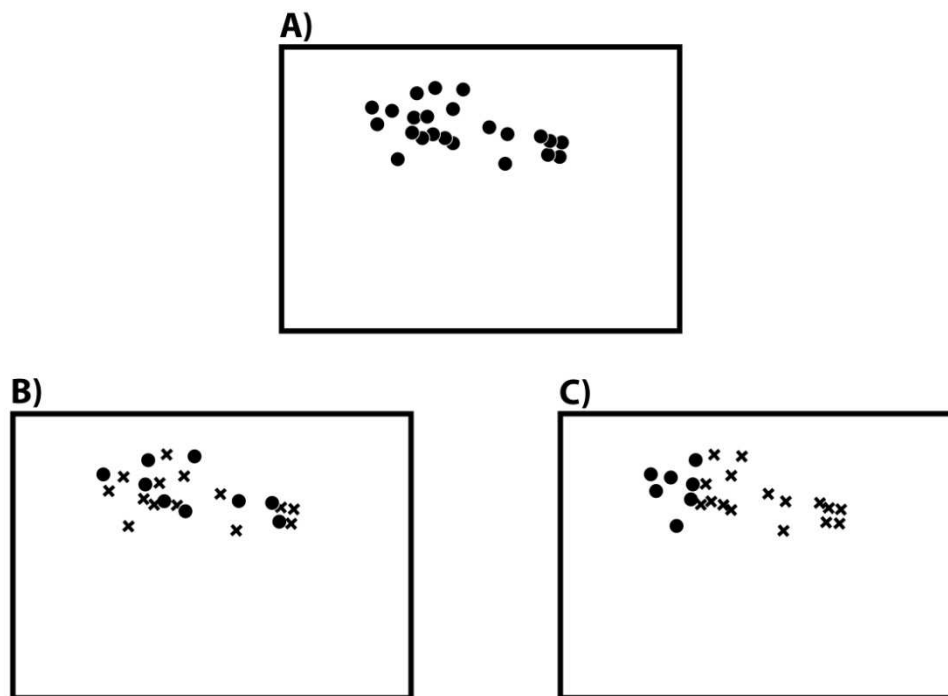


Figure 3. Hypothetical models of pre-extinction cimolodontan morphospace occupation, based on understanding of morphospace dynamics under selective and non-selective extinction as discussed by Wills (2001). Circles represent surviving species, while X's represent extinct species. A) Pre-extinction morphospace occupation by sampled members of the Late Cretaceous North American Cimolodonta. B) Random extinction: In the case of random extinction, nearest neighbor distances and inter- species variance should increase as morphospace becomes less densely occupied. Note that range of morphospace occupation is mostly preserved. C) Non-random (selective) extinction: Variance and nearest neighbor distance values will change, though it is difficult to say if they will increase or decrease. The most notable change is the decrease in range. Here, strong selection has taken place against morphological characteristics accounted for by the first eigenvector – the x-axis – with losses limited to species expressing the negatively selected phenotype. A second subgroup of species express positively selected characters, and are spared from extinction. Range of occupied morphospace has decreased.

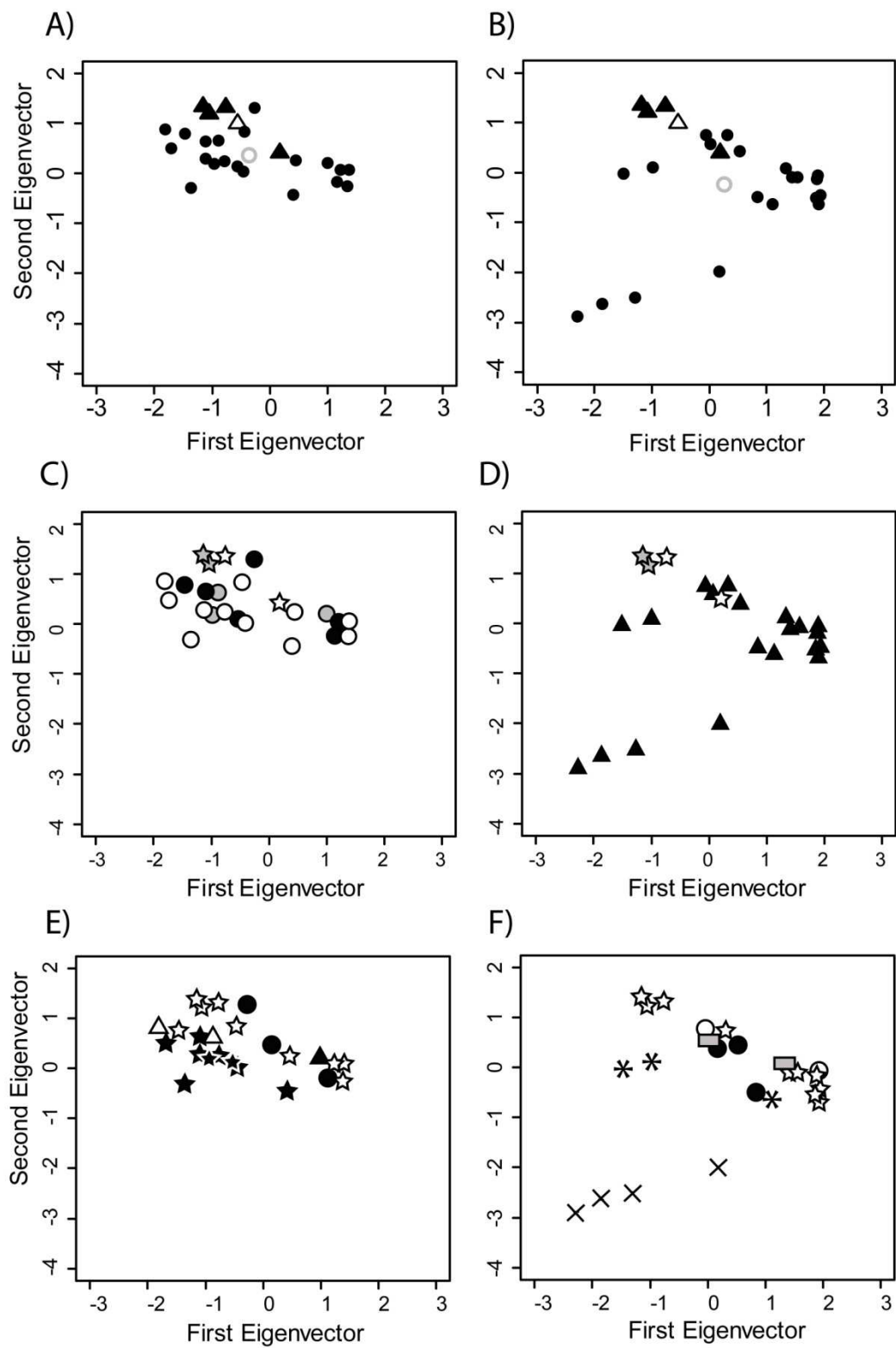


Figure 4. Pre and post-extinction morphospace groups. Morphospace occupation is plotted on the two most explanatory eigenvectors (first eigenvector: 21.06% variance explained; second eigenvector: 12.50% of variance explained) (table 1). A & B) Species that survive the K-Pg extinction are represented with black triangles; the white-filled triangle represents the centroid for these survivor species in A and B. White-filled circles represent the centroid of species unique to the pre and post-extinction Cimolodonta, respectively. A) Late Cretaceous species (pre-extinction) (black circles) are plotted with extinction survivor species (solid black triangles). B) Puercan species (post-extinction) (black circles) and species which survived the K-Pg extinction (solid black triangles). Note the expansion in occupied morphospace in the Puercan relative to the Late Cretaceous. C & D) Morphospace occupation, with age groups distinguished. C) Late Cretaceous species morphospace. Black circles: Judithian; gray-filled circles: Late Cretaceous; white-filled circles: Latest Cretaceous; white-filled stars: Latest Cretaceous and Puercan; gray-filled stars: Late Cretaceous and Puercan. D) Puercan morphospace, with black triangles representing species originating in the Puercan. White-filled stars: Latest Cretaceous and Puercan; gray-filled stars: Late Cretaceous and Puercan. E & F) Classifications of taxa in morphospace. E) Late Cretaceous taxa. Circles: *Cimexomys* (Cimolodonta incertae sedis); white-filled stars: Neoplagiaulacidae; black stars: Cimolomyidae; white-filled triangles: Cimolodontidae; black triangles: *Paracimexomys*. F) Puercan taxa. X's: Taeniolabididae; white-filled circles: Ptilodontidae; asterisks: Eucosmodontidae; white-filled stars: Neoplagiaulacidae; black circle: *Cimexomys* (Cimolodonta incertae sedis); gray-filled boxes: Microcosmodontidae.

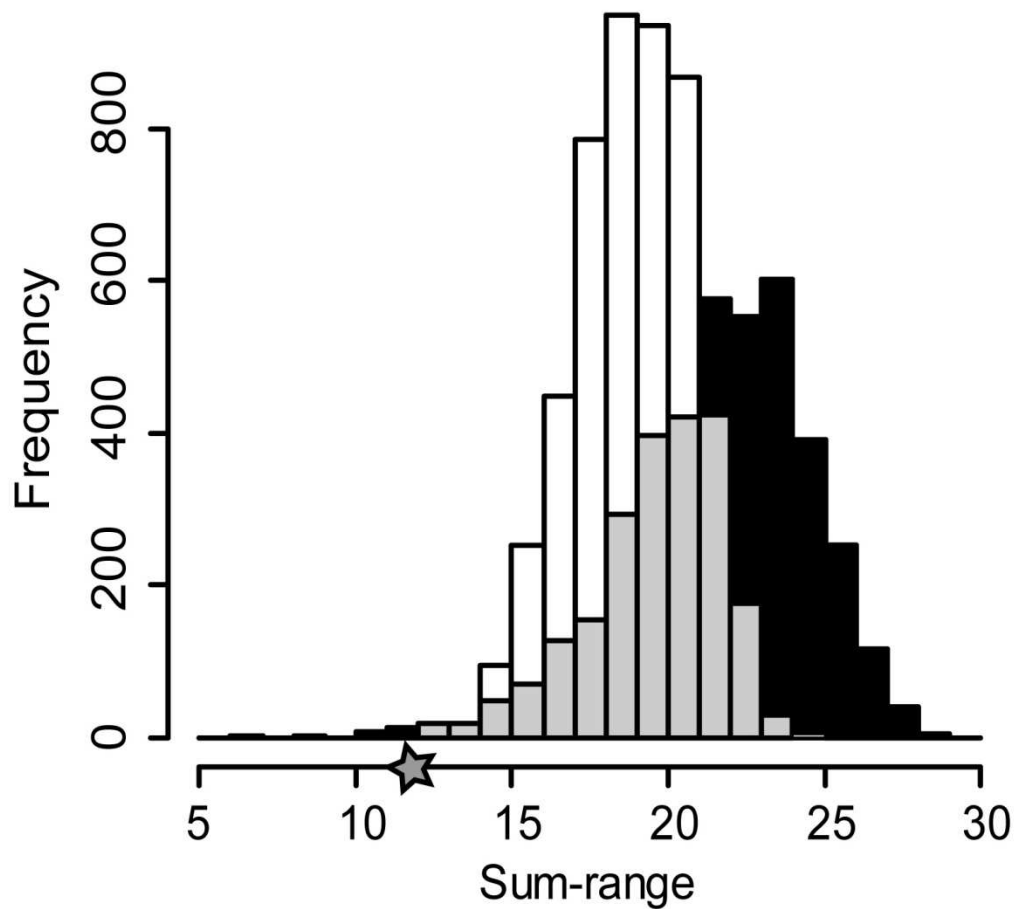


Figure 5. Histogram derived from the jackknife of sum-ranges, with frequencies of sum-range values from 5000 samples, without replacement within each sample, of four species per sampling. The star represents the sum-range value of the four extinction survivor species (12.17). White bars represent frequency of sum-range values for Judithian, Edmontonian, and Lancian species; black bars represent frequency of sum-range values for Puercan; grey regions show the area of overlap between pre and post extinction species sum-range frequencies. By randomly sampling four species per resample, the random versus non-random nature of the multituberculate extinction is addressed with respect to occupied morphospace sum-range over 17 eigenvectors. Analysis of the sum-range distribution test shows that the reduction of cimolodontan sum-range during the K-Pg extinction is significant ( $P = 0.0006$ ).

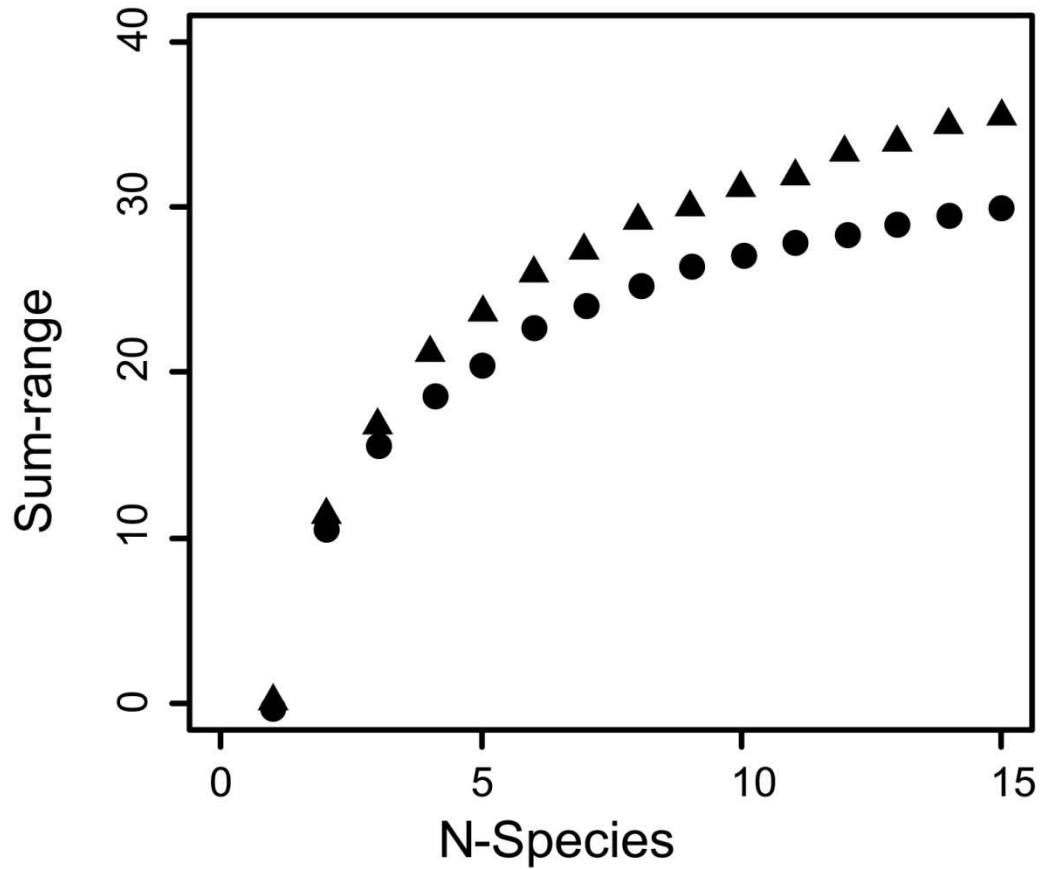


Figure 6. Rarefaction of sum-ranges for Late Cretaceous species (circles), and Puercan species (triangles). The rarefaction took place over the course of 100 permutations of range-sampling; the number of species (n-species) are increased iteratively from 2 to 15. Morphospace range is measured over the 17 most explanatory eigenvectors (table 1), accounting for 90.94% of the total variance. The rarefaction applies the range metric of disparity to consecutively increasing random samples of species. Increased sum-range of pre-extinction and post-extinction species is evident even at small n- species values and increases as species were added. The disparity in range across 17 eigenvectors is in agreement with the increase in range of occupied morphospace from the Late Cretaceous to the Puercan seen in Figure 4.

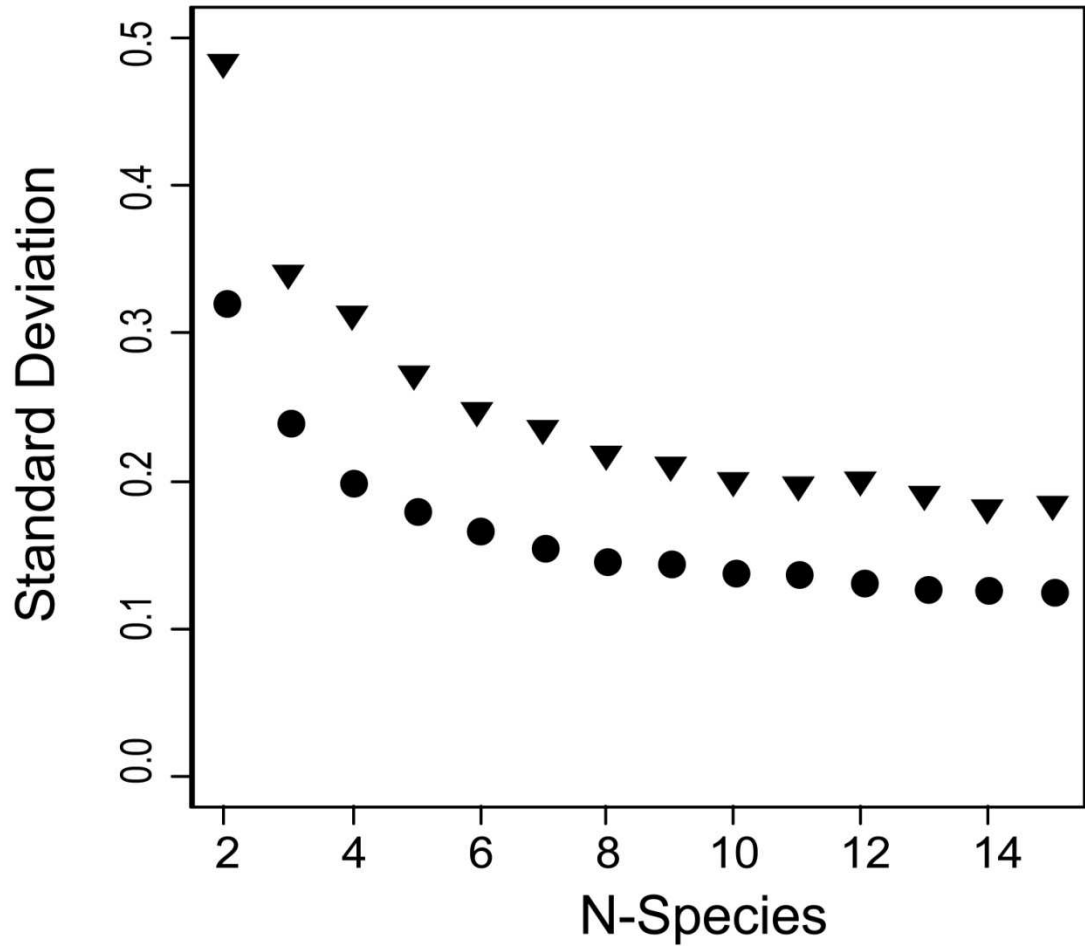


Figure 7. Rarefaction of variance (standard deviation) for Late Cretaceous species (circles), and Puercan species (triangles). The rarefaction took place over 1000 permutations of variance sampling; the number of species (n-species) are increased iteratively from 2 to 15. Variance is measured over the 17 most explanatory eigenvectors, accounting for 90.94% of the total variation in the Euclidian distance matrix analyzed by the PCO (table 1). The rarefaction applies the variance metric of disparity to consecutively increasing random samples of species. Variance values remain higher for post-extinction species regardless of sample size. The disparity in variance across 17 eigenvectors is in agreement with the increase in taxa dispersion from pre-extinction to post-extinction seen in Figure 4.

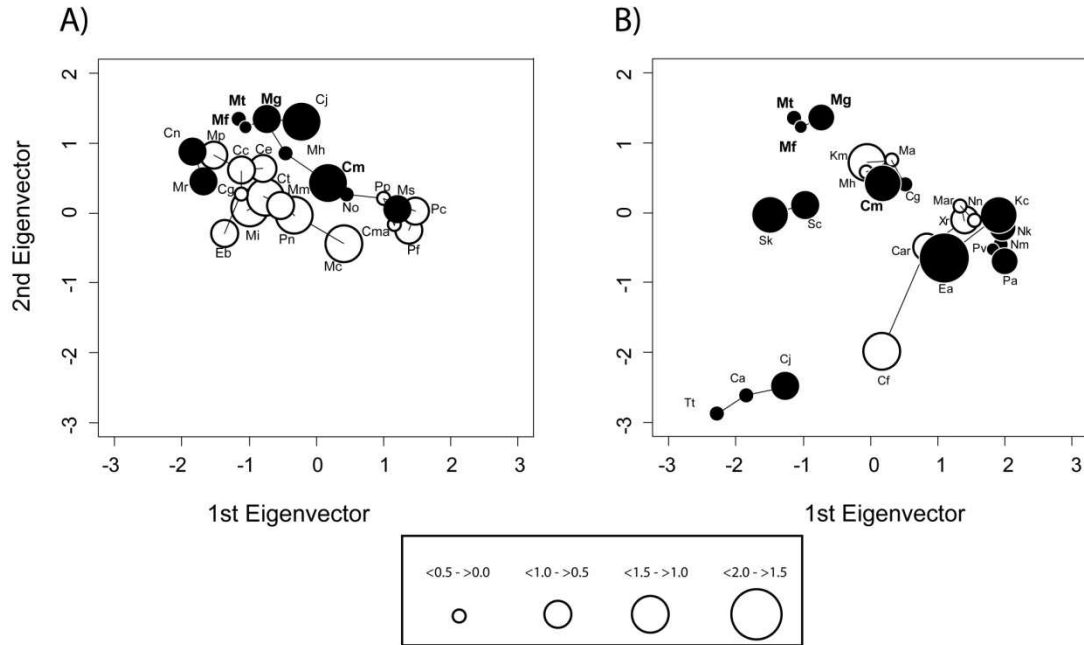


Figure 8. Nearest neighbor distances (NND) between species in a three dimensional morphospace. The three dimensions are the three most explanatory eigenvectors of the principal coordinates analysis (PCO) performed on the Euclidean distance transformation of a binary morphological character matrix. These first three eigenvectors account for 43.04% of the total variance in the morphospace (Table 1). The first eigenvector describes 21.06% of the total variance; the second eigenvector describes 12.50% of the total variance; the third eigenvector describes 9.5% of the variance (Table 1). Lines connect nearest neighboring points within the three dimensional morphospace. The Z-axis is visualized through diameter and shade of points within the scatterplot; point-diameter decreases with decreasing absolute value along the Z-axis; points with negative values are open, while positive values are shaded black. Categories of third axis values are shown in the figure key. The nearest neighbor distances approximate morphological similarity between any two species within the defined morphospace. Underlined species are acknowledged as having  $<1/3$  of the total coded characters accounted for. A) Late Cretaceous species NND's. Abbreviated species names are defined as follows: Cc: *Cimolomys clarki*; Ce: *Cimolodon electus*; Cg: *Cimolomys gracilis*; Cj: *Cimexomys judithae*; Cm: *Cimexomys*



magnus; Cm: *Cimexomys minor*; Cn: *Cimolodon nitidus*; Ct: *Cimolomys trochuus*; Eb: *Essonodon browni*; Mc: *Meniscoessus collomensis*; Mf: *Mesodma formosa*; Mg: *Mesodma garfieldensis*; Mh: *Mesodma hensleighi*; Mi: *Meniscoessus intermedius*; Mm: *Meniscoessus major*; Mp: *Mesodma primaeva*; Mr: *Meniscoessus robustus*; Ms: *Mesodma senecta*; Mt: *Mesodma thompsoni*; No: *Nidimys occultus*; Pc: *Parikimys carpenteri*; Pf: *Parectypodus foxi*; Pn: *Paressonodon nelsoni*; Pp: *Paracimexomys priscus*. B) Puercan species NND's. Abbreviated species names are defined as follows: Ca: *Catopsalis alexanderi*; Car: *Cimexomys arapahoensis*; Cf: *Catopsalis foliatus*; Cg: *Cimexomys gratus*; Cj: *Catopsalis joyneri*; Cm: *Cimexomys minor*; Ea: *Eucosmodon americanus*; Kc: *Kimbetohia campi*; Km: *Kimbetohia mziae* Ma: *Mesodma ambigua*; Mar: *Microcosmodon arcuatus*; Mf: *Mesodma formosa*; Mg: *Mesodma garfieldensis*; Mh: *Microcosmodon harleyi*; Mt: *Mesodma thompsoni*; Nk: *Neoplagiaulax kremnus*; Nm: *Neoplagiaulax macintyreii*; Nn: *Neoplagiaulax nelsoni*; Pa: *Parectypodus armstrongi*; Pv: *Parectypodus vanvaleni*; Sc: *Stygimys camptorhiza*; Sk: *Stygimys kuszmauli*; Tt: *Taeniolabis taoensis*; Xr: *Xyronomys robinsoni*.

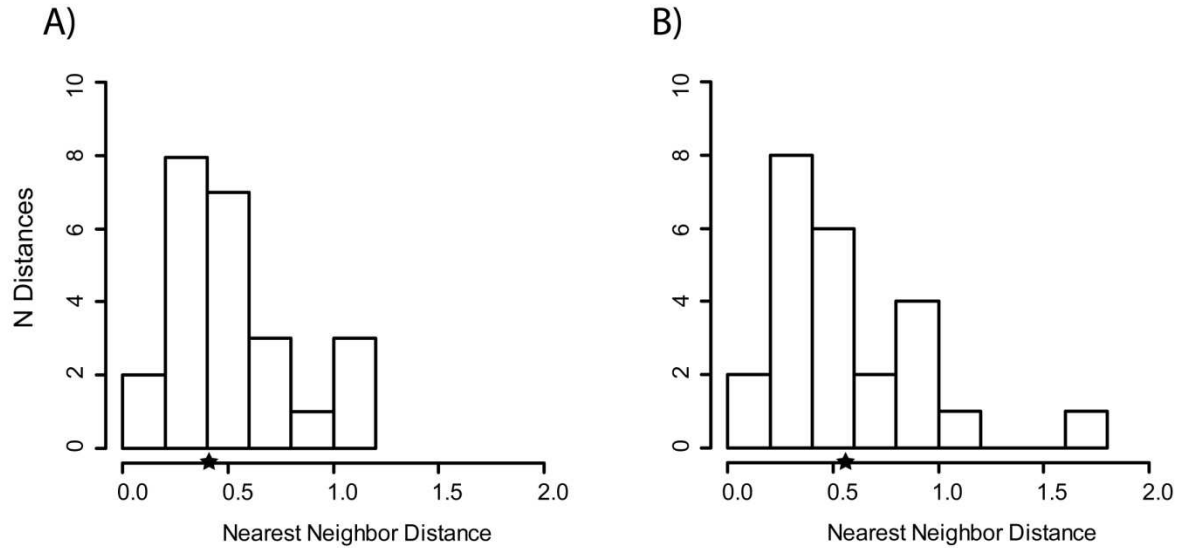


Figure 9. Histograms of nearest neighbor distances (NND) for A) Late Cretaceous species, and B) Puercan species. Distances are measured between species within a three dimensional morphospace. The three dimensions are the three most explanatory eigenvectors of the PCO analysis performed on the Euclidean distance transformation of the binary morphological character matrix. Together, they account for 43.04% of the total variance in the morphospace. The nearest neighbor distances approximate morphological similarity between any two species within the three-dimensional morphospace. Across the K-Pg extinction boundary, abundance and distribution of distances shift slightly toward greater NNDs. The stars are positioned at the geometric mean value of NND for Late Cretaceous species (A), and Puercan species (B). NND increase in the Puercan relative to the Late Cretaceous is non-significant ( $P = 0.9342$ ).

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## APPENDICES

Appendix 1: Species-specific faunal ages and stratigraphic ranges. PBDB indicates use of the Paleobiology Database, with the date of most recent access given (4/23/2013). For all species, a direct search from the PBDB homepage search tool using the genus/species name was used to locate the stratigraphic and faunal age ranges for each species. Stratigraphic and faunal age ranges are unchanged from original PBDB access in September 2011 and May 2012. Stratigraphic and faunal age ranges are restricted to the portions of the Campanian (Judithian, Edmontonian), Maastrichtian (Edmontonian, Lancian), and Danian (Puercan) focused on in this study. The full ranges of *Cimolodon electus*, *Mesodma senecta*, *Paracimexomys priscus*, *Neoplagiaulax macintyreii*, *Neoplagiaulax nelsoni*, and *Mesodma thompsoni* extend beyond the ranges used in this study. Conferred specimens and specimens with dubious referrals have not been included in the data set.

Species	North American Faunal Stage Range	Stratigraphic Range	Sources
<i>Catopsalis alexanderi</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Catopsalis foliatus</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Catopsalis joyneri</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Cimexomys arapahoensis</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Cimexomys gratus</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Cimexomys judithae</i>	Judithian	Campanian	PBDB accessed 4/23/2013; modified (Weil, pers. comm., September, 2011).
<i>Cimexomys magnus</i>	Judithian	Campanian	PBDB accessed 4/23/2013
<i>Cimexomys minor</i>	Lancian, Puercan	Maastrichtian, Danian	PBDB accessed 4/23/2013
<i>Cimolodon electus</i>	Judithian, Edmontonian	Campanian, Maastrichtian	PBDB accessed 4/23/2013
<i>Cimolodon nitidus</i>	Edmontonian, Lancian	Campanian, Maastrichtian	PBDB accessed 4/23/2013; modified (Weil, pers. comm., July, 2012).

Species	North American Faunal Stage Range	Stratigraphic Range	Sources
<i>Cimolomys clarki</i>	Judithian	Campanian	PBDB accessed 4/23/2013
<i>Cimolomys gracilis</i>	Edmontonian, Lancian	Campanian, Maastrichtian	PBDB accessed 4/23/2013
<i>Cimolomys trochuus</i>	Lancian	Maastrichtian	PBDB accessed 4/23/2013
<i>Essonodon browni</i>	Lancian	Maastrichtian	PBDB accessed 4/23/2013
<i>Eucosmodon americanus</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Kimbetohia campi</i>	Puercan	Danian	PBDB accessed 4/23/2013; modified (Weil, pers. comm., July, 2012).
<i>Kimbetohia mziae</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Meniscoessus collomensis</i>	Edmontonian	Campanian, Maastrichtian	PBDB accessed 4/23/2013
<i>Meniscoessus intermedius</i>	Judithian, Edmontonian	Campanian, Maastrichtian	PBDB accessed 4/23/2013
<i>Meniscoessus major</i>	Judithian	Campanian	PBDB accessed 4/23/2013
<i>Meniscoessus robustus</i>	Edmontonian, Lancian	Campanian, Maastrichtian	PBDB accessed 4/23/2013
<i>Mesodma ambigua</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Mesodma formosa</i>	Judithian, Edmontonian, Lancian, Puercan	Campanian, Maastrichtian, Danian	PBDB accessed 4/23/2013
<i>Mesodma garfieldensis</i>	Lancian, Puercan	Maastrichtian, Danian	PBDB accessed 4/23/2013
<i>Mesodma hensleighi</i>	Lancian	Maastrichtian	PBDB accessed 4/23/2013; modified in accordance with Cifelli et al. (2004), and Ogg (2012)
<i>Mesodma primaeva</i>	Judithian	Campanian	PBDB accessed 4/23/2013
<i>Mesodma senecta</i>	Judithian	Campanian	PBDB accessed 4/23/2013

Species	North American Faunal Stage Range	Stratigraphic Range	Sources
<i>Mesodma thompsoni</i>	Lancian, Puercan	Maastrichtian, Danian	PBDB accessed 4/23/2013; modified in accordance with Cifelli et al. (2004).
<i>Microcosmodon arcuatus</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Microcosmodon harleyi</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Neoplagiaulax kremnus</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Neoplagiaulax macintyreii</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Neoplagiaulax nelsoni</i>	Puercan	Danian	Weil and Krause (2007)
<i>Nidimys occultus</i>	Edmontonian	Campanian, Maastrichtian	PBDB accessed 4/23/2013
<i>Paracimexomys priscus</i>	Judithian, Edmontonian, Lancian	Campanian, Maastrichtian	PBDB accessed 4/23/2013
<i>Parectypodus armstrongi</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Parectypodus foxi</i>	Lancian	Maastrichtian	PBDB accessed 4/23/2013
<i>Parectypodus vanvaleni</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Paressonodon nelsoni</i>	Lancian	Maastrichtian	PBDB accessed 4/23/2013
<i>Parikimys carpenteri</i>	Lancian	Maastrichtian	PBDB accessed 4/23/2013
<i>Stygimys camptorhiza</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Stygimys kuszmauli</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Taeniolabis taoensis</i>	Puercan	Danian	PBDB accessed 4/23/2013
<i>Xyronomys robinsoni</i>	Puercan	Danian	PBDB accessed 4/23/2013

Appendix 2: Morphological character data assembled by Dr. Anne Weil.

Species	1	2	3	4	5	6	7	8	9	10	11	12
<i>Catopsalis alexanderi</i>	?	?	1	1	0	1	1	?	0	?	1	1
<i>Catopsalis foliatus</i>	?	?	?	?	?	?	1	?	0	?	1	1
<i>Catopsalis joyneri</i>	1	1	1	1	0	?	0	0	0	?	1	1
<i>Cimexomys arapahoensis</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Cimexomys gratus</i>	?	?	?	?	?	?	0	0	?	0	0	0
<i>Cimexomys judithae</i>	?	?	?	?	0	1	0	0	?	0	0	0
<i>Cimexomys magnus</i>	?	?	?	?	?	?	?	?	?	?	0	?
<i>Cimexomys minor</i>	1	1	?	?	0	1	0	0	?	0	0	0
<i>Cimolodon electus</i>	?	?	?	?	?	?	?	?	?	1	0	0
<i>Cimolodon nitidus</i>	1	1	1	0	0	1	0	0	?	0	0	0
<i>Cimolomys clarki</i>	1	1	?	?	?	?	0	0	?	0	0	0
<i>Cimolomys gracilis</i>	?	?	?	?	?	?	0	0	?	0	0	0
<i>Cimolomys trochuus</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Essonodon browni</i>	1	1	?	?	?	?	?	?	?	?	?	?
<i>Eucosmodon americanus</i>	?	?	1	1	1	?	1	?	?	?	0	0
<i>Kimbetohia campi</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Kimbetohia mziae</i>	?	?	?	?	?	?	0	0	?	0	0	0
<i>Meniscoessus collomensis</i>	?	?	?	?	?	1	?	?	?	?	?	?
<i>Meniscoessus intermedius</i>	?	?	?	?	?	1	?	?	?	?	?	?
<i>Meniscoessus major</i>	?	?	?	?	0	1	0	0	?	0	0	0
<i>Meniscoessus robustus</i>	1	1	0	?	0	1	0	0	?	0	0	0
<i>Mesodma ambigua</i>	1	0	1	0	0	1	0	0	?	1	0	0
<i>Mesodma formosa</i>	1	0	1	0	0	1	0	0	?	0	0	0
<i>Mesodma garfieldensis</i>	1	0	?	?	0	1	0	0	?	0	0	0
<i>Mesodma hensleighi</i>	1	0	?	?	0	1	?	?	?	0	0	0
<i>Mesodma primaeva</i>	1	0	1	0	0	1	?	?	?	0	0	0
<i>Mesodma senecta</i>	1	0	?	?	?	1	?	?	?	1	0	0
<i>Mesodma thompsoni</i>	1	0	?	?	0	1	0	0	?	0	0	0
<i>Microcosmodon arcuatus</i>	?	?	?	?	?	?	0	0	1	?	0	0
<i>Microcosmodon harleyi</i>	?	?	?	?	?	?	0	0	1	?	0	0
<i>Neoplagiaulax kremnus</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Neoplagiaulax macintyreii</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Neoplagiaulax nelsoni</i>	?	?	?	?	?	?	0	0	?	1	0	0
<i>Nidimys occultus</i>	?	?	?	?	0	1	0	0	?	0	0	0
<i>Paracimexomys priscus</i>	?	?	?	?	?	?	0	0	?	0	0	?
<i>Parectypodus armstrongi</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Parectypodus foxi</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Parectypodus vanvaleni</i>	?	?	?	?	?	?	?	?	?	0	0	0
<i>Paessonodon nelsoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parikimys carpenteri</i>	?	?	?	?	?	?	0	0	?	0	0	0
<i>Stygimys camptorhiza</i>	?	?	1	1	1	?	1	?	?	0	0	0
<i>Stygimys kuszmauli</i>	1	1	1	1	1	1	1	?	?	0	0	0
<i>Taeniolabis taoensis</i>	1	1	1	1	0	1	1	?	0	?	1	1
<i>Xyromys robinsoni</i>	?	?	?	?	?	?	?	?	?	0	0	0
Species	13	14	15	16	17	18	19	20	21	22	23	24
<i>Catopsalis alexanderi</i>	1	0	0	1	?	0	0	?	1	1	0	1
<i>Catopsalis foliatus</i>	1	0	?	?	?	?	?	?	?	?	?	?
<i>Catopsalis joyneri</i>	1	0	0	1	?	0	?	1	1	0	?	?

<i>Cimexomys arapahoensis</i>	0	0	?	1	?	1	?	?	?	?	?	?
<i>Cimexomys gratus</i>	0	0	1	0	?	0	0	?	?	?	?	?
<i>Cimexomys judithae</i>	0	0	1	0	1	0	0	?	?	?	?	1
<i>Cimexomys magnus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cimexomys minor</i>	0	?	?	0	1	0	0	?	?	?	?	?
<i>Cimolodon electus</i>	0	?	?	0	?	0	0	?	?	?	?	?
<i>Cimolodon nitidus</i>	0	1	1	0	1	0	0	?	?	?	?	1
<i>Cimolomys clarki</i>	0	?	0	0	1	0	0	1	?	?	?	?
<i>Cimolomys gracilis</i>	0	?	0	0	0	0	0	?	?	?	?	?
<i>Cimolomys trochuus</i>	0	?	0	0	1	0	?	?	?	?	?	?
<i>Essonodon browni</i>	?	?	?	?	?	1	0	?	?	?	?	?
<i>Eucosmodon americanus</i>	0	?	1	0	?	1	?	?	?	?	?	1
<i>Kimbetohia campi</i>	0	?	1	0	1	?	?	?	?	?	?	?
<i>Kimbetohia mziae</i>	0	1	1	0	?	1	0	?	?	?	?	?
<i>Meniscoessus collomensis</i>	?	?	?	?	?	0	0	?	?	?	?	?
<i>Meniscoessus intermedius</i>	?	?	?	?	?	0	0	?	?	?	?	?
<i>Meniscoessus major</i>	0	1	?	0	0	0	0	?	?	?	?	?
<i>Meniscoessus robustus</i>	0	1	0	0	1	0	0	0	?	?	0	1
<i>Mesodma ambigua</i>	0	1	0	0	1	0	?	?	?	?	?	?
<i>Mesodma formosa</i>	0	?	0	0	1	0	0	?	?	?	?	?
<i>Mesodma garfieldensis</i>	0	?	0	0	1	0	0	?	?	?	?	?
<i>Mesodma hensleighi</i>	0	?	0	0	?	0	0	?	?	?	?	?
<i>Mesodma primaeva</i>	0	?	0	0	1	0	0	?	?	?	?	?
<i>Mesodma senecta</i>	0	?	0	?	1	0	?	?	?	?	?	?
<i>Mesodma thompsoni</i>	0	?	0	0	1	0	0	?	?	?	?	?
<i>Microcosmodon arcuatus</i>	1	?	1	0	1	1	0	?	?	?	?	?
<i>Microcosmodon harleyi</i>	1	?	0	1	1	0	0	?	?	?	?	?
<i>Neoplagiaulax kremnus</i>	0	?	1	?	1	?	?	?	?	?	?	?
<i>Neoplagiaulax macintyreii</i>	0	?	1	?	1	?	?	?	?	?	?	?
<i>Neoplagiaulax nelsoni</i>	0	?	1	0	0	?	?	?	?	?	?	?
<i>Nidimys occultus</i>	0	1	1	0	?	0	?	?	?	?	?	?
<i>Paracimexomys priscus</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parectypodus armstrongi</i>	1	?	1	?	1	?	?	?	?	?	?	?
<i>Parectypodus foxi</i>	0	1	?	0	?	0	0	?	?	?	?	?
<i>Parectypodus vanvaleni</i>	0	?	1	0	?	?	?	?	?	?	?	?
<i>Paressonodon nelsoni</i>	?	?	?	?	?	?	?	?	?	?	?	?
<i>Parikimys carpenteri</i>	0	1	1	0	1	1	0	?	?	?	?	?
<i>Stygimys camptorhiza</i>	0	?	1	1	1	1	?	?	?	?	?	?
<i>Stygimys kuszmauli</i>	0	0	1	0	0	1	0	1	0	?	1	?
<i>Taeniolabis taoensis</i>	1	0	0	1	1	0	0	1	1	1	0	?
<i>Xyronomys robinsoni</i>	0	1	1	0	?	1	0	?	?	?	?	?

Species	25	26	27	28	29	30	31	32	33	34	35
<i>Catopsalis alexanderi</i>	?	1	?	0	?	?	1	?	?	?	?
<i>Catopsalis foliatus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Catopsalis joyneri</i>	?	1	?	0	?	?	0	0	?	?	1
<i>Cimexomys arapahoensis</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Cimexomys gratus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Cimexomys judithae</i>	?	0	1	0	1	0	0	1	0	?	0
<i>Cimexomys magnus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Cimexomys minor</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Cimolodon electus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Cimolodon nitidus</i>	?	0	1	?	?	?	0	1	0	?	0
<i>Cimolomys clarki</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Cimolomys gracilis</i>	?	?	?	?	?	?	0	1	0	?	1
<i>Cimolomys trochuus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Essonodon browni</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Eucosmodon americanus</i>	?	1	?	0	1	1	0	1	0	?	1
<i>Kimbetohia campi</i>	?	0	?	0	1	0	0	1	1	0	0
<i>Kimbetohia mziae</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Meniscoessus collomensis</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Meniscoessus intermedius</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Meniscoessus major</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Meniscoessus robustus</i>	?	0	1	0	1	0	0	1	0	?	0
<i>Mesodma ambigua</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Mesodma formosa</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Mesodma garfieldensis</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Mesodma hensleighi</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Mesodma primaeva</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Mesodma senecta</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Mesodma thompsoni</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Microcosmodon arcuatus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Microcosmodon harleyi</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Neoplagiaulax kremnus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Neoplagiaulax macintyreii</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Neoplagiaulax nelsoni</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Nidimys occultus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Paracimexomys priscus</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Parectypodus armstrongi</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Parectypodus foxi</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Parectypodus vanvaleni</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Paressonodon nelsoni</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Parikimys carpenteri</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Stygimys camptorhiza</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Stygimys kuszmauli</i>	?	0	1	?	?	?	?	?	?	?	?
<i>Taeniolabis taoensis</i>	?	1	?	0	?	?	1	?	?	?	?
<i>Xyronomys robinsoni</i>	?	?	?	?	?	?	?	?	?	?	?

Species	36	37	38	39	40	41	42	43	44	45	46
<i>Catopsalis alexanderi</i>	0	1	1	1	1	0	1	0	1	1	1
<i>Catopsalis foliatus</i>	?	?	1	1	1	1	?	?	?	?	?
<i>Catopsalis joyneri</i>	?	1	1	1	1	0	1	0	1	1	0
<i>Cimexomys arapahoensis</i>	?	?	1	0	?	?	?	?	?	?	?
<i>Cimexomys gratus</i>	0	1	1	0	?	?	0	?	1	0	?
<i>Cimexomys judithae</i>	0	1	1	0	?	?	1	0	1	1	0
<i>Cimexomys magnus</i>	0	1	1	0	?	?	0	?	1	0	?
<i>Cimexomys minor</i>	0	1	1	0	?	?	1	0	1	0	?
<i>Cimolodon electus</i>	0	1	1	1	0	?	1	0	1	1	0
<i>Cimolodon nitidus</i>	0	1	1	1	0	?	1	0	1	1	1
<i>Cimolomys clarki</i>	0	1	1	0	?	?	1	0	1	1	0
<i>Cimolomys gracilis</i>	0	1	1	1	0	?	1	0	1	1	1
<i>Cimolomys trochuus</i>	?	?	1	1	0	?	1	0	1	1	0
<i>Essonodon browni</i>	?	1	1	1	1	0	1	0	1	1	1
<i>Eucosmodon americanus</i>	0	1	?	?	?	?	?	?	?	?	?
<i>Kimbetohia campi</i>	1	1	?	?	?	?	?	?	?	?	?
<i>Kimbetohia mziae</i>	?	?	1	0	?	?	1	0	1	1	0
<i>Meniscoessus collomensis</i>	?	?	1	1	1	0	?	?	?	?	?
<i>Meniscoessus intermedius</i>	?	?	1	1	0	?	1	0	1	1	0
<i>Meniscoessus major</i>	0	1	1	1	1	0	1	0	?	?	?
<i>Meniscoessus robustus</i>	0	1	1	1	1	0	1	0	1	1	1
<i>Mesodma ambigua</i>	?	?	1	0	?	?	?	?	?	?	?
<i>Mesodma formosa</i>	0	1	1	0	?	?	1	0	1	1	0
<i>Mesodma garfieldensis</i>	0	1	1	0	?	?	1	0	1	1	0
<i>Mesodma hensleighi</i>	0	1	1	0	?	?	1	0	1	1	0
<i>Mesodma primaeva</i>	0	?	1	1	0	?	1	0	1	1	0
<i>Mesodma senecta</i>	0	1	?	?	?	?	?	?	?	?	?
<i>Mesodma thompsoni</i>	0	1	1	0	?	?	1	0	1	1	0
<i>Microcosmodon arcuatus</i>	?	?	1	0	?	?	?	?	?	?	?
<i>Microcosmodon harleyi</i>	0	1	1	0	?	?	0	?	1	1	0
<i>Neoplagiaulax kremnus</i>	1	1	?	?	?	?	?	?	?	?	?
<i>Neoplagiaulax macintyreii</i>	?	?	?	?	?	?	?	?	?	?	?
<i>Neoplagiaulax nelsoni</i>	?	?	1	0	?	?	?	?	?	?	?
<i>Nidimys occultus</i>	0	1	1	0	?	?	1	0	?	?	?
<i>Paracimexomys priscus</i>	?	?	1	0	?	?	0	?	1	0	?
<i>Parectypodus armstrongi</i>	1	1	?	?	?	?	?	?	?	?	?
<i>Parectypodus foxi</i>	?	?	1	0	?	?	?	?	?	?	?
<i>Parectypodus vanvaleni</i>	0	1	?	?	?	?	?	?	?	?	?
<i>Paressonodon nelsoni</i>	?	?	1	1	0	?	1	0	1	1	1
<i>Parikimys carpenteri</i>	?	?	1	0	?	?	?	?	?	?	?
<i>Stygimys camptorhiza</i>	0	1	1	1	0	?	1	0	1	1	0
<i>Stygimys kuszmauli</i>	0	1	1	1	0	?	1	0	1	1	0
<i>Taeniolabis taoensis</i>	0	0	1	1	1	1	1	0	1	1	1
<i>Xyronomys robinsoni</i>	?	?	1	0	?	?	?	?	?	?	?

Species	47	48	49	50	51	52	53	54	55	56
<i>Catopsalis alexanderi</i>	0	1	?	1	0	0	0	0	0	1
<i>Catopsalis foliatus</i>	?	1	?	?	0	0	0	1	0	1
<i>Catopsalis joyneri</i>	0	0	?	0	0	0	0	0	0	1
<i>Cimexomys arapahoensis</i>	?	1	?	1	0	0	0	1	0	?
<i>Cimexomys gratus</i>	0	1	1	0	0	0	0	1	1	1
<i>Cimexomys judithae</i>	0	0	1	1	0	0	0	0	1	1
<i>Cimexomys magnus</i>	0	?	?	?	0	0	?	?	1	?
<i>Cimexomys minor</i>	?	0	?	0	0	0	0	0	1	?
<i>Cimolodon electus</i>	0	1	?	1	0	1	0	1	1	1
<i>Cimolodon nitidus</i>	0	1	0	1	0	1	0	1	1	1
<i>Cimolomys clarki</i>	0	1	0	1	0	1	1	1	1	1
<i>Cimolomys gracilis</i>	0	1	0	1	0	1	0	1	0	1
<i>Cimolomys trochuus</i>	0	1	?	1	0	1	0	1	?	1
<i>Essonodon browni</i>	0	1	0	1	1	?	0	1	0	1
<i>Eucosmodon americanus</i>	?	0	?	1	0	0	0	0	1	?
<i>Kimbetohia campi</i>	?	?	?	?	?	?	?	?	?	?
<i>Kimbetohia mziae</i>	0	0	?	1	0	1	0	1	1	1
<i>Meniscoessus collomensis</i>	?	?	0	1	0	1	0	0	?	1
<i>Meniscoessus intermedius</i>	0	1	?	1	0	1	0	1	?	1
<i>Meniscoessus major</i>	0	1	0	1	0	1	0	1	0	1
<i>Meniscoessus robustus</i>	0	1	0	1	0	1	0	1	0	0
<i>Mesodma ambigua</i>	?	?	1	1	0	1	0	1	1	?
<i>Mesodma formosa</i>	0	0	1	1	0	1	0	1	0	1
<i>Mesodma garfieldensis</i>	0	0	1	1	0	0	0	1	1	1
<i>Mesodma hensleighi</i>	0	0	1	1	0	0	0	?	0	1
<i>Mesodma primaeva</i>	0	1	1	1	0	1	1	1	1	1
<i>Mesodma senecta</i>	?	?	?	?	?	?	?	?	?	?
<i>Mesodma thompsoni</i>	0	1	1	1	0	1	?	1	1	1
<i>Microcosmodon arcuatus</i>	?	?	1	1	0	1	1	0	0	?
<i>Microcosmodon harleyi</i>	0	?	1	1	0	1	1	0	0	1
<i>Neoplagiaulax kremnus</i>	?	?	?	?	?	?	?	?	?	?
<i>Neoplagiaulax macintyreii</i>	?	?	?	?	?	?	?	?	?	?
<i>Neoplagiaulax nelsoni</i>	?	?	?	?	?	?	?	?	0	1
<i>Nidimys occultus</i>	?	1	?	1	0	0	0	0	0	1
<i>Paracimexomys priscus</i>	1	0	1	1	0	0	0	0	1	0
<i>Parectypodus armstrongi</i>	?	?	?	?	?	?	?	?	?	?
<i>Parectypodus foxi</i>	?	?	?	0	0	0	0	0	1	1
<i>Parectypodus vanvaleni</i>	?	?	?	?	?	?	?	?	?	?
<i>Paressonodon nelsoni</i>	0	0	0	1	0	1	?	0	?	1
<i>Parikimys carpenteri</i>	?	?	?	1	0	0	0	0	0	1
<i>Stygimys camptorhiza</i>	0	0	1	1	0	1	0	1	0	1
<i>Stygimys kuszmauli</i>	0	0	1	1	0	0	0	1	0	1
<i>Taeniolabis taoensis</i>	0	1	?	0	0	0	0	1	0	1
<i>Xyronomys robinsoni</i>	?	?	?	0	0	1	0	?	0	1



Species	57	58	59	60
<i>Catopsalis alexanderi</i>	0	?	0	?
<i>Catopsalis foliatus</i>	0	?	?	?
<i>Catopsalis joyneri</i>	0	?	0	?
<i>Cimexomys arapahoensis</i>	?	?	?	?
<i>Cimexomys gratus</i>	0	?	1	0
<i>Cimexomys judithae</i>	1	0	1	0
<i>Cimexomys magnus</i>	?	?	?	?
<i>Cimexomys minor</i>	?	?	1	0
<i>Cimolodon electus</i>	0	?	1	0
<i>Cimolodon nitidus</i>	0	?	1	0
<i>Cimolomys clarki</i>	0	?	?	?
<i>Cimolomys gracilis</i>	0	?	1	0
<i>Cimolomys trochuus</i>	0	?	?	?
<i>Essonodon browni</i>	1	1	?	?
<i>Eucosmodon americanus</i>	?	?	1	0
<i>Kimbetohia campi</i>	?	?	1	0
<i>Kimbetohia mziae</i>	1	0	?	?
<i>Meniscoessus collomensis</i>	0	?	?	?
<i>Meniscoessus intermedius</i>	0	?	?	?
<i>Meniscoessus major</i>	0	?	1	0
<i>Meniscoessus robustus</i>	?	?	1	0
<i>Mesodma ambigua</i>	?	?	?	?
<i>Mesodma formosa</i>	1	0	1	0
<i>Mesodma garfieldensis</i>	1	0	1	0
<i>Mesodma hensleighi</i>	1	0	1	0
<i>Mesodma primaeva</i>	0	?	0	?
<i>Mesodma senecta</i>	?	?	1	0
<i>Mesodma thompsoni</i>	0	?	1	0
<i>Microcosmodon arcuatus</i>	?	?	?	?
<i>Microcosmodon harleyi</i>	1	0	1	0
<i>Neoplagiaulax kremnus</i>	?	?	1	0
<i>Neoplagiaulax macintyreii</i>	?	?	0	?
<i>Neoplagiaulax nelsoni</i>	1	0	1	0
<i>Nidimys occultus</i>	0	?	1	0
<i>Paracimexomys priscus</i>	?	?	?	?
<i>Parectypodus armstrongi</i>	?	?	0	?
<i>Parectypodus foxi</i>	0	?	?	?
<i>Parectypodus vanvaleni</i>	?	?	0	?
<i>Paressonodon nelsoni</i>	1	1	?	?
<i>Parikimys carpenteri</i>	1	0	?	?
<i>Stygimys camptorhiza</i>	0	?	1	0
<i>Stygimys kuszmauli</i>	0	?	1	0
<i>Taeniolabis taoensis</i>	0	?	?	?
<i>Xyronomys robinsoni</i>	1	0	?	?

Appendix 3: Morphological characters and character states provided by Dr. Anne Weil.

1) enamel ultrastructure

0\_\_\_\_\_ preprismatic

1\_\_\_\_\_ prismatic

2) prismatic enamel

0\_\_\_\_\_ small prismatic or intermediate

1\_\_\_\_\_ gigantoprismatic

3) enamel covering of lower incisor

0\_\_\_\_\_ uniform thickness

1\_\_\_\_\_ non-uniform thickness

4) non-uniform enamel thickness on lower incisor

0\_\_\_\_\_ thicker on labial surface

1\_\_\_\_\_ restricted to labial surface

5) compression of lower incisor

0\_\_\_\_\_ not laterally compressed

1\_\_\_\_\_ laterally compressed

6) P/2 present/absent

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

7) P/3 present /absent

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

8) P/3 cusp number if P/3 is present

0\_\_\_\_\_ 1-2 cusps

1\_\_\_\_\_ 3-5 cusps

9) P/4 number of serrations

0\_\_\_\_\_ less than or equal to 4

1\_\_\_\_\_ more than 4 but less than or equal to 7

10) P/4 number of serrations greater than 7

0\_\_\_\_\_ 8-14 serrations

1\_\_\_\_\_ 15 or more serrations

11) lateral ridges on P/4

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

12) P/4 crest shape

0\_\_\_\_\_ rounded

1\_\_\_\_\_ triangular

13) P/4 crest shape, rounded or blade-like

0\_\_\_\_\_ crown longer than high

1\_\_\_\_\_ crown height and length subequal

14) vertical position of the unworn P/4 serrate edge in relation to the unworn molar tooth row.

0\_\_\_\_\_ below

1\_\_\_\_\_ level or above

15) P/4 posterolabial cusps

0\_\_\_\_\_ prominent

1\_\_\_\_\_ reduced

16) P/4 posterolabial shelf

0\_\_\_\_\_ anterior width of tooth greater than posterior width

1\_\_\_\_\_ posterior width of tooth greater than or equal to anterior width

17) size of P/4 roots (diameter/circumference)

0\_\_\_\_\_ equal in size

1\_\_\_\_\_ anterior larger

18) M/1 cusp rows diverge

0\_\_\_\_\_ don't diverge

1\_\_\_\_\_ diverge

19) M/2 w/ central basin

0\_\_\_\_\_ no central basin

1\_\_\_\_\_ central basin

20) I2/ cusp count

0\_\_\_\_\_ 4

1\_\_\_\_\_ 3 or fewer

21) I2/ enamel uniform

0\_\_\_\_\_ uniform

1\_\_\_\_\_ not uniform

22) I2/ enamel if not uniform

0\_\_\_\_\_ thicker labially than lingually

1\_\_\_\_\_ restricted to labial surface

23) I3/ location

0\_\_\_\_\_ on margin of palate

1\_\_\_\_\_ near midline of palate

24) P0/ present or absent

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

25) P0/ number of cusps

0\_\_\_\_\_ 4 cusps

1\_\_\_\_\_ fewer than 4 cusps

26) P1/ present or absent

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

27) P1/ cusp count

0\_\_\_\_\_ 4 cusps

1\_\_\_\_\_ fewer than 4 cusps

28) P2/ present or absent

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

29) P2/ number of cusps if P2/ present

0\_\_\_\_\_ 5-6 cusps

1\_\_\_\_\_ 3-4 cusps

30) P2/ number of roots if P2/ present

0\_\_\_\_\_ 2 roots

1\_\_\_\_\_ 1 root



31) P3/ present or absent

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

32) P3/ cusps if p3/ present, part 1

0\_\_\_\_\_ cusps 1:2

1\_\_\_\_\_ cusps > 1:2

33) P3/ cusps if p3/ present, part 2

0\_\_\_\_\_ cusps 2:2

1\_\_\_\_\_ cusps > 2:3

34) P3/ cusps if p3/ present, part 3

0\_\_\_\_\_ cusps 2:4

1\_\_\_\_\_ cusps 3:4

35) P3/ number of roots if p3/present

0\_\_\_\_\_ 2 roots

1\_\_\_\_\_ 1 root

36) p4/ posterobasal cusps

0\_\_\_\_\_ present

1\_\_\_\_\_ absent

37) P4/ number of roots

0\_\_\_\_\_ 1

1\_\_\_\_\_ 2

38) M1/ length (proxy for body size)

0\_\_\_\_\_ <2mm

1\_\_\_\_\_ greater than or equal to 2mm

39) M1/ length (proxy for body size), part 2

0\_\_\_\_\_ greater than or equal to 2mm and less than 4 mm

1\_\_\_\_\_ greater than or equal to 4mm

40) M1/ length (proxy for body size), part 3

0\_\_\_\_\_ greater than or equal to 4mm and less than 6.5 mm

1\_\_\_\_\_ greater than or equal to 6.5 mm

41) M1/ length (proxy for body size), part 4

0\_\_\_\_\_ greater than or equal to 6.5 mm and less than 11 mm

1\_\_\_\_\_ greater than or equal to 11 mm

42) M1/ number of cusps in median row

0\_\_\_\_\_ < 6

1\_\_\_\_\_ between 6 and 11 cusps

43) M1/ number of cusps in median row

0\_\_\_\_\_ <11

1\_\_\_\_\_ >11

44) M1/ internal cusp row

0\_\_\_\_\_ internal row absent

1\_\_\_\_\_ internal row present

45) M1/ length of internal cusp row compared to total M1/ length (internal row present)

0\_\_\_\_\_ <50% length of tooth

1\_\_\_\_\_ greater than or equal to 50%, but less than 80%

46) M1/ length of internal cusp row compared to total M1/length (present, long)

0\_\_\_\_\_ <80%

1\_\_\_\_\_ 80% or greater

47) median and external rows of M1/ diverge

0\_\_\_\_\_ parallel – do not diverge

1\_\_\_\_\_ diverge anteriorly

48) M2/number of cusps in the internal row

0\_\_\_\_\_ fewer than 4 cusps

1\_\_\_\_\_ 4 cusps or more

49) M1/1 have multiple accessory roots

0\_\_\_\_\_ yes

1\_\_\_\_\_ no

50) M1/1 cusp arrangement

0\_\_\_\_\_ cusps side-by-side across the tooth

1\_\_\_\_\_ cusps staggered, creating a sinuous median valley

51) molar cusp shape (M1/1); cusp base of equal or subequal A-P and M-L dimensions

0\_\_\_\_\_ equal or subequal

1\_\_\_\_\_ ridge-like

52) molar cusp shape (M1/1); (cusp base of equal or subequal A-P and M-L dimensions)

0\_\_\_\_\_ conical or quadrangular

1\_\_\_\_\_ subcrescentic, crescentic, or recurved

53) M/1 and M/2 have notch posterior to internal row

0\_\_\_\_\_ absent

1\_\_\_\_\_ present

54) Crown ornamentation – molar cusps grooved or ridged

0\_\_\_\_\_ absent

1\_\_\_\_\_ present

55) P4/M1/ length ratio

0\_\_\_\_\_ less than or equal to .8

1\_\_\_\_\_ greater than .8

56) M/1: M/2 length ratio

0\_\_\_\_\_ less than or equal to 1

1\_\_\_\_\_ greater than 1

57) M/1: M/2 length ratio greater than 1

0\_\_\_\_\_ greater than 1 and less than or equal to 1.5

1\_\_\_\_\_ greater than 1.5

58) M/1: M/2 length ratio greater than 1

0\_\_\_\_\_ greater than 1.5 and less than or equal to 2

1\_\_\_\_\_ greater than 2

59) P/4:P4/ length ratio

0\_\_\_\_\_ less than or equal to 1.1

1\_\_\_\_\_ greater than 1.1

60) P/4:P4/ length ratio greater than 1.1

0\_\_\_\_\_ less than or equal to 1.8

1\_\_\_\_\_ greater than 1.8



VITA

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Thesis: A MORPHOSPACE ODDITY: ASSESSING MORPHOLOGICAL  
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